A TEMPORAL COMPARISON OF THE EELGRASS (*ZOSTERA MARINA* L.) FOOD WEB AND COMMUNITY STRUCTURE AT IZEMBEK LAGOON, ALASKA FROM THE MID-1970'S TO 2008

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A

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Abstract

This thesis investigates food web and community structure in Izembek Lagoon, Alaska, an ecologically important sub-arctic seagrass system. Unprecedented environmental changes in high latitudes, such as increased sea-surface temperatures and a shorter duration of shore-fast sea ice, may now favor seagrass over phytoplankton production as compared to forty years ago. Any resulting shifts in food web and community dynamics could have substantial consequences given the importance of seagrass habitat for Alaskan fisheries, global migratory bird populations and benthic energy transformation. Recent (2008) stable isotope (C and N) values and benthic community metrics were gathered and compared to results from a similar study from the mid-1970's to gauge temporal food web and community structure differences. An increase in reliance on seagrass carbon was detected in organisms involved in detrital and sediment processing. An increase in abundance of certain benthic organisms and a decrease in overall community evenness were also seen. These findings suggest an escalation in delivery of seagrass carbon to the food web, possibly induced by changing seagrass morphology or bed density at this location.

Table of Contents

Page

Signature Page i

Title Page ii

Abstract iii

Table of Contents iv

List of Figures vi

List of Tables vii

List of Appendices viii

Acknowledgments ix

Chapter 1 General Introduction 1

1.1 Seagrasses and Their Functions 1

1.2 References 4

Chapter 2 A comparison of carbon stable isotopic variation in a sub-arctic eelgrass (*Zostera marina* L.) food web sampled in 1947–1976 vs. 2008 11

2.1 Abstract 11

2.2 Introduction 12

2.3 Methods 14

2.3.1 Study Site 14

2.3.2 Sample Collection and Treatment 14

2.3.3 $\delta^{13}C$ Mixing Model 17

2.3.4 Statistical Analysis of Carbon Isotope Data 18

2.3.5 Trophic Structure 18

2.4 Results 18

2.4.1 Temporal Carbon Comparison 18

2.4.2 $\delta^{13}C$ Mixing Model 19

2.4.3 Trophic Structure 19

2.5 Discussion 20

2.6 Conclusion 24
2.7 References 24
Chapter 3 Temporal comparison reveals a shift in the benthic eelgrass (*Zostera marina* L.) community from 1977 compared to 2008 at Izembek Lagoon, Alaska 44
3.1 Abstract 44
3.2 Introduction 45
3.3 Methods 47
3.3.1 Study Site 47
3.3.2 Sampling Design 47
3.3.3 Comparison of Data Sets 48
3.4 Results 49
3.5 Discussion 50
3.6 Conclusion 55
3.7 References 56
Appendices 75
Chapter 4 General Conclusion 77
4.1 Synthesis and Implications for Izembek Lagoon 77
4.2 References 79

List of Figures

Page

Figure 2.1: Izembek Lagoon and surrounding wilderness area (hatch pattern), Alaska. Peninsula, U.S.A.34

Figure 2.2: Sampling transect at Grant Point showing relative depth strata. 35

Figure 2.3: The frequency distribution of historic and modern $\delta^{13}C$ values in 24 benthic species from the Izembek Lagoon food web, Alaska 36

Figure 2.4: Linear regression of $\delta^{13}C$ values from historic and modern lipid normalized tissues (dotted line, $R^2 = 0.3951$) 37

Figure 2.5: Mean $\delta^{13}C$ values (± 1 SD) of grouped taxa in 1974 –'76 and 2008 38

Figure 2.6: Mean $\delta^{13}C$ values (± 1 SD) of organisms grouped by consumer category in 1974 –'76 and 2008....... 38

Figure 2.7: Stable carbon and nitrogen isotope values for primary producers (open box), and fauna (closed box) from 2008 shown as taxonomic categories 39

Figure 3.1: Izembek Lagoon region of the Alaska Peninsula 67

Figure 3.2: Sampling transect at Grant Point showing relative depth strata. 68

Figure 3.3: Multidimensional scaling shows greater similarities in averaged faunal density per station in the benthic community between 1977 and 1977* groups than between 2008 and either 1977 or 1977* 69

Figure 3.4: Mean faunal evenness (± 1 SD) in 2008 and 1977 shown with Pielou's index at stations along the sampling transect 70

Figure 3.5: Mean biodiversity (± 1 SD) in 2008 and 1977 shown with the Shannon-Wiener index at stations along the sampling transect 70

Figure 3.6: Mean species richness (± 1 SD) in 2008 and 1977 shown with Margalef's index at stations along the sampling transect 71

Figure 3.7: Mean faunal density (± 1 SD) at stations along the sampling transect 71

Figure 3.8: Comparison of aggregated taxonomic group density as recorded from sediment cores in 2008 (white bars, n = 15) and 1977 (grey bars, n = 27) 72

Figure 3.9: Taxon density as a percentage of total individuals sampled in historic (1977) and modern (2008) sediment cores from the Izembek Lagoon benthos 73

List of Tables

Page

Table 2.1: Mean $\delta^{13}C$ values (±1 SD) of primary producers in 2008 and 1974–'76 40

Table 2.2 Stable isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of organisms collected from Izembek Lagoon eelgrass ecosystem presented as (n) replicates with standard deviations (±1 SD). 41

Table 2.3: Mixing model results of carbon partitioning in the organisms of Izembek Lagoon showing three levels of possible trophic level fractionation and an organism's corresponding reliance on eelgrass carbon………….. 43

Table 3.1: One-way crossed ANOSIM (Analysis of Similarities) testing similarity of average faunal density between 1977* (rarified 1977 data set), 1977, and 2008 stations on a historic transect 74

Table 3.2: One-way ANOVA (Analysis of Variance) tests between common biodiversity indices for benthic community data sets at Izembek Lagoon in 1977 and 1977* (rarified 1977 data set)......................74

Table 3.3: Results of a BEST matching test between 1977 and 2008 for community abundances of taxa…………….. 74

List of Appendices

Page

Appendix 3.1: Abundance of organisms (individuals per m^2) at stations on the Grant Point long-term transect in 1977 at Izembek Lagoon 75

Appendix 3.2: Abundance of organisms (individuals per m^2) at stations on the Grant Point long-term transect in 2008 76

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Chapter 1: General Introduction

1.1 Seagrasses and Their Functions

Seagrasses are marine angiosperms that grow in the shallow embayments and estuaries of all continents but Antarctica (Phillips and Menez 1988). As ‘ecosystem engineers’, seagrasses physically alter their surrounding environment by creating a slow-moving boundary layer above the substrate (Fonseca et al. 1983; Jones et al. 1994). This significantly reduces water speed, causes increased sedimentation of particulate matter and fine materials (Orth 1977; Bos et al. 2007), and enhances benthic nutrient availability (Kenworthy et al. 1982). Dense seagrass canopies also attenuate waves (Koch et al. 2006a), which results in a subsequent decrease in shoreline erosion (Bos et al. 2007), augmented by the sediment binding action of seagrass roots and rhizomes within the bed. These interactions between seagrasses and their fluid medium create a positive feedback mechanism (Koch et al. 2006b; van der Heide et al. 2011), favorably altering environmental conditions (substrate and nutrient availability, water column clarity and light penetration) that support maximum seagrass growth and production.

Numerous waterfowl, fish and invertebrate herbivores are directly supported by seagrass primary productivity (Williams and Heck 2001), and rich food webs are built upon detritally processed seagrass carbon (Al-Maslamani et al. 2012). Because of the cellulose content of seagrass, direct consumption of vegetative parts is generally limited to organisms with terrestrial origins (e.g., birds, manatee, dugong) that have adaptations for digesting cellulose (Thayer et al. 1984; Bjorndal 1985). In some seagrass systems large amounts of carbon are passed through the food web or transferred to terrestrial and pelagic systems by direct herbivory (Heck et al. 2008), although on average this number is just over 18% of net primary seagrass production (Duarte and Cebrian 1996). More commonly, over 50% of seagrass carbon is decomposed (Duarte and Cebrian 1996), and then passed through food webs via the detrital loop where it is made labile through microbial processing (Harrison 1989). Considering seagrasses cover only 0.15% of the oceans’ surface area (Charpy-Roubaud and Sournia, 1990) and contribute only 1% to the net global ocean primary productivity, their 12% contribution to net ocean ecosystem production (Duarte and Cebrian 1996) is proportionally very high. This small global coverage is also highly valuable as a habitat, especially for juvenile fishes, crabs, and shrimp (Harris et al. 2008).

As ‘coastal nurseries’ (Heck et al. 2003), seagrass habitats tend to have high associated biodiversity compared with non-vegetated habitats (Gullström et al. 2008). The three-dimensional complexity provided by seagrass leaves and rhizomes creates shelter and refuge from predators for small organisms and juvenile fish and invertebrates (Connolly 1994; Klumpp and Kwak 2005; Sirota and Hovel 2006). Their abundance within the habitat in turn provides feeding opportunities for higher trophic levels. Additionally, the stabilizing effect of roots and rhizomes modifies infaunal habitat, increasing oxygen penetration, stabilizing sediments, and decreasing predation for infaunal and epifaunal organisms (Orth 1977). Seagrass refugia have a significantly positive effect on juvenile fish and invertebrate survival and growth compared to other habitats (Ryer 1987; Pihl et al. 2006), to the extent that it is considered essential fish habitat by managers including in the State of Alaska (Johnson and Thedinga 2005).

Eelgrass (*Zostera marina* L.) is the most wide-ranging seagrass species in the Northern Hemisphere (den Hartog 1970; Green and Short 2003), and plays a major role in overall community biodiversity and abundance in temperate coastal ecosystems (Pihl et al. 2006). Along with global seagrass populations (Duarte 2002; Lotze et al. 2006), eelgrass has undergone declines along the populated coasts of North America and Europe (Keser et al. 2003; Pihl et al. 2006). Human use patterns are directly involved in most cases of seagrass decline (Orth et al. 2006; Boudouresque et al. 2009), although indirect stressors like climate change have also been implicated (Seddon et al. 2000). Often, these anthropogenic impacts occur from land development (Lotze et al. 2006), which can increase sediment and nutrient levels in runoff that feeds seagrass areas (Keser et al. 2003; Strom and Klaveness 2003), causing die-offs from subsequent phytoplankton blooms that decrease water clarity (Hauxwell et al. 2003). Other major impacts include diseases (Short et al. 1988), damage from recreational boat use (Creed and Amado 1999; Engeman et al. 2008), and importation of invasive species (Williams 2007). Loss of eelgrass through direct or indirect damage results in lower abundance and biodiversity within the ecosystem (Reed and Hovel 2006). Relatively unpopulated areas are usually exceptions to this trend, and persist as healthy, functioning ecosystems (Hughes et al. 2002). One such remote system is Izembek Lagoon, Alaska.

Located on the Alaska Peninsula (U.S.A.), Izembek Lagoon (55º14′40″N, 162º55′00″W) is recognized as the largest contiguous eelgrass bed in the world (McRoy 1966). As an embayment of the Bering Sea, sea surface temperatures in the lagoon average -3.6ºC (Bond and Adams 2002) and sea ice covers >75% of the lagoon for 1–2 months between December and March (Ward et al. 1997). More northerly eelgrass populations are known (e.g., Hopavägen Lagoon, Norway; 63º35′65″N, 9º32′80″E; Duarte et al. 2002) but are influenced by the North Atlantic with winter sea surface temperatures typically exceeding 6°C and with mostly ice-free coastal conditions between December and March. Approximately 13,690 ha of Izembek Lagoon's 34,662 ha are covered with eelgrass, a spatial distribution that has remained relatively stable for at least three decades (Ward et al. 1997). The Izembek Lagoon eelgrass bed is a productive ecosystem that supports important ecological functions and rich nursery grounds, which in turn support species important to the Bristol Bay and Southeastern Bering Sea commercial fisheries (Tack 1970). These include Pacific herring (*Clupea pallasii*), juvenile Pacific cod (*Gadus macrocephalus*), juvenile rockfish (*Sebastes spp*.), and juvenile Pacific salmon (*Oncorhynchus spp.*) (Tack 1970; Dean et al. 2000; Byerly 2001; Johnson et al. 2003; National Oceanic and Atmospheric Administration 2011). In addition to fisheries species, half a million waterfowl and more than a quarter million shorebirds visit Izembek's eelgrass beds in the spring and fall (Tibbits et al. 1996). The abundant food and refuge of the lagoon impart tremendous value as a staging area for migratory birds from many paths including the North American Pacific, East Asian-Australasian and West Pacific Flyways (U.S. Fish and Wildlife Service 1985).

Izembek Lagoon has been acknowledged as a biologically and economically important ecosystem, and subsequently protected as a State Game Refuge (Alaska Department of Fish and Game 2010) insulated from human impacts by the surrounding Izembek National Wildlife Refuge. Since this first designation of protection in 1972, the lagoon and eelgrass beds have been internationally recognized by the Convention on Wetlands of International Importance in 1986 and became the first "Wetland of International Importance" in the United States. In 2001, it was designated, along with adjacent Moffet Lagoon, by the American Bird Conservancy as a Globally Important Bird Area (Sowl and Poetter 2004). Despite protection by federal law and of the global conservation community, a pending campaign for local development could still affect Izembek's eelgrass ecosystem. In 2010, a land exchange was signed into law that allows a road through the adjacent Izembek National Wildlife Refuge to connect the community of King Cove with an airport (Edgamon 2010; Tanis 2011). The road will cross streams and wetlands that feed into the lagoon, and access will undoubtedly increase off-road vehicle use and access for hunting, boating, fishing, and tourism (Sowl and Poetter 2004). In addition to these pressures, the road itself poses water quality challenges if not maintained. Considering the lagoon's uniqueness, and its key role in global bird migration and Bering Sea fisheries, pre-development documentation of temporal stability of food web dynamics and benthic biodiversity is crucial for future monitoring efforts.

Along with direct human effects such as road construction, climate change has also been suggested as a driver influencing sensitive seagrass communities (Orth et al. 2006). At Izembek Lagoon, an increase in overwintering waterfowl populations have been positively correlated with decreasing sea ice cover concurrent with a ~1°C temperature increase since 1962 (Ward et al. 2008). In the adjacent Bering Sea, bottom temperature and sea ice retreat play a role in reorganization of community distribution and structure and changing biogeography (Mueter and Litzow 2008). Retreating sea ice, increasing temperatures and increased CO_2 concentrations may be facilitating pole-ward expansion for seagrasses in the northern hemisphere (Palacios and Zimmerman 2007; Virnstein and Hall 2009). However, negative effects of ocean acidification on seagrass fauna (Orr et al. 2005; Hall-Spencer et al. 2008), mechanical damages by increased storm intensity and duration (Scavia et al. 2002), and overall sea level rise may counteract any positive effects gained from climate changes (Short and Neckles 1999; Orth et al. 2006).

The goal of this study was to examine whether the food web structure and biodiversity associated with the far north Izembek Lagoon eelgrass ecosystem has changed since the first ecosystem study at Izembek Lagoon in the early1970's (McConnaughey and McRoy 1979). In chapter 2 of this thesis, I present an investigation of the food web structure at Izembek Lagoon using stable carbon and nitrogen isotope analysis. I gauge the present use of primary production by select organisms in the food web and provide a modern trophic benchmark of Izembek's eelgrass food web structure. Using stable carbon isotope data from the early 1970's, I assess if alterations in the food web may have occurred, especially with respect to the sources of primary production, and provide a hypothesis of why carbon-use patterns have changed and how this may relate to overall climate factors in the sub-arctic. In chapter 3, I present an assessment of benthic community structure in 2008 and compare these data with similar data from the mid-1970's to test for temporal stability of Izembek Lagoon's eelgrass associated benthos. Using these results, I explore how projected climate and ocean conditions may affect the modern benthic species assemblage, and consider possible consequences to higher trophic levels. Chapter 4 describes what these findings may mean to the success of this globally important, high-northern eelgrass ecosystem.

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Chapter 2: A comparison of carbon stable isotopic variation in a sub-arctic eelgrass (*Zostera marina* L.) food web sampled in 1947–1976 vs. 2008[1]

2.1 Abstract

Climate-related conditions in Bering Sea surface waters, such as a rising concentration of CO_2 (*aq*) and a shorter duration of shore-fast ice, may be increasingly favoring seagrass over phytoplankton production as compared to forty years ago. Carbon stable isotope compositions ($\delta^{13}C$ values) of organisms in an eelgrass ecosystem at Izembek Lagoon, Alaska collected in 2008 were compared to those from a similar study conducted in the mid 1970's to examine whether temporal shifts in production and food web structure have occurred. This comparison showed a relatively stable food web with organisms continuing to rely on a mixture of carbon from lagoon eelgrass and phytoplankton. However, some consumer groups (detrital, deposit and filter feeders) and benthic taxa (polychaetes, shrimp and unsegmented worms) had an increased proportional contribution from eelgrass carbon in their diets. These findings suggest an increase in available eelgrass carbon compared with phytoplankton from the 1970s to 2008. The nitrogen stable isotope composition of the 2008 community (not available in the 1970's study) revealed a four tier trophic structure. These results document carbon and nitrogen stable isotope compositions in a sub-arctic eelgrass bed that can be used for further monitoring and future comparisons with other seagrass food webs.

[1] Tippery, A. C. A comparison of carbon stable isotopic variation in a sub-arctic eelgrass (*Zostera marina* L.) food web sampled in 1947–1976 vs. 2008. Prepared for submission to 'Estuaries and Coasts'

2.2 Introduction

Seagrass ecosystems provide invaluable ecological and economic services (Heck et al. 2003; Orth et al. 2006) such as coastal stabilization (Koch et al. 2006), carbon production and sequestration (Duarte et al. 2005), wave attenuation (Fonseca and Fisher 1986), and the provision of a three-dimensional habitat (Heck and Orth 1980; Sirota and Hovel 2006). Of these services, primary production may become even more important with the effects of anthropogenic climate change (Duarte and Chiscano 1999). The global net community production of seagrass meadows ranges from approximately 550–1100 g C m^{-2} y^{-1} (Hemminga and Duarte 2000). Along with phytoplankton in temperate oceans (70–180 g C m^{-2} y^{-1}), kelp ecosystems (649–1800 g C m^{-2} y^{-1}), and coral reefs (1,500–3,700 g C m^{-2} y^{-1}) (Castro and Huber 2003), seagrass ecosystems are a significant contributor to marine primary production. While increasing surface seawater temperature and decreasing pH are predicted to cause challenges for phytoplankton, kelps and corals (Bellwood et al. 2004; Andersson et al. 2008; Wernberg et al. 2010), seagrasses are expected to benefit from these changes (Zimmerman et al. 1997; Palacios and Zimmerman 2007; Hall-Spencer et al. 2008). This is because many seagrasses are very plastic in their response to temperature differences (Phillips and Lewis 1983) and as a group they exhibit a broader thermal tolerance range than other nearshore ecosystems such as corals, kelps, mangroves and salt marshes (Green and Short 2003). Seagrasses are usually carbon limited (but see Beer et al. 2002), using diffusion of CO_2 across cellular boundaries for at least 50% of the carbon used in photosynthesis (Durako 1993; Beer and Koch 1996; Beer and Rehnberg 1997), and would benefit from increased CO_2 saturation in surface seawater (Beer and Koch 1996).

Prior investigations have documented regime shifts that arise with disruptions in seagrass primary production (Harris and Tyrrell 2001; Orth et al. 2006; Reed and Hovel 2006). Regime shifts can cause a change in character within an ecosystem from one stable state to another (Folke et al. 2004), many times centering on the loss or gain of foundational species (e.g., seagrass, kelps, coral). Regime shifts in seagrass systems are typically brought on by eutrophication, which increases the abundance of competing phytoplankton, fouling epiphytes, and macroalgae (Hemminga and Duarte 2000) and limits the ability of seagrass to photosynthesize (Hauxwell et al. 2003; Lee et al. 2007). When seagrass production declines and there is an increase in abundance of competing producers, changes in upper trophic levels quickly follow (Viaroli et al. 2008; Jiao 2009). Examples of seagrass food web reorganization caused by such primary production regime shifts are well documented in both Chesapeake (Kemp et al. 2005) and Florida Bays, U.S.A. (Folke et al. 2004), and western Sweden (Pihl et al. 2006). A similar post-regime shift pattern in these three study locations was a decrease in abundance and biodiversity of mezo-grazers and/or small demersal fishes commonly fed upon by upper trophic levels. The ultimate result of loss of seagrass primary production was decreased abundance and biodiversity of economically important fisheries.

Regime shifts such as these may not be possible to reverse once in motion (Scheffer et al. 2001). Monitoring for incremental food web alterations leading up to regime shifts would be helpful in averting or planning for broad ecosystem changes (Folke et al. 2004). The use of stable isotopes to monitor seagrass organisms and their consumption of primary production could be a valuable tool in this regard.

Carbon stable isotopes are useful in determining the relative importance of multiple types of primary production and their trophic pathways in a food web (McConnaughey and McRoy 1979; Kharlamenko et al. 2001; Jaschinski et al. 2008). Nitrogen stable isotopes can distinguish trophic positions of organisms within a food web (Hemminga and Mateo 1996; Hobson and Wassenaar 1999; Iken et al. 2005). Together, carbon and nitrogen stable isotopes can reveal both shifts in carbon sources and reorganization of organisms in a food web through temporal comparisons. One caveat is that all sources of primary production must be known and be distinct from each other in terms of their ^{13}C:^{12}C ratios, expressed as $\delta^{13}C$‰ (per mil) values. An organism's stable carbon isotope signature, or $\delta^{13}C$ value, is essentially dictated by the stable carbon isotopic composition of its food sources (Phillips and Koch 2002; Lepoint et al. 2004). Trophic fractionation due to assimilation only produces a relatively minor increase (0.8 ± 1.1‰) in the $\delta^{13}C$ value of an organism relative to its diet (DeNiro and Epstein 1978; Owens 1987; Hobson and Welch 1992). Nitrogen stable isotope signatures (^{14}N:^{15}N ratio) are expressed as $\delta^{15}N$‰ (per mil) values, and increase at a predicted rate of ~3.8‰ with increasing trophic position (e.g., Hobson and Welch 1992). They have been used to map trophic connections in marine food webs (Hobson and Welch 1992; Iken et al. 2005) and temperate seagrass systems in particular (Kharlamenko et al. 2001; Jaschinski et al. 2008). Interpretation of $\delta^{15}N$ values can sometimes be problematic because the predicted fractionation rate can vary by diet quality and with animal groups (Lepoint et al. 2004). Mapping carbon and nitrogen stable isotopes together in a food web creates an integrated picture of the diets and trophic position of its residents, and a baseline to test for changes in food web architecture.

The earliest sub-arctic study using stable carbon isotopes to map a seagrass food web was conducted at Izembek Lagoon, a large embayment on the Bering Sea coast of the Alaska Peninsula (McConnaughey and McRoy 1979). This early study documented $\delta^{13}C$ values for a suite of organisms and evaluated the proportional contribution of eelgrass relative to phytoplankton in their diets. The outcome was a structural snapshot of the lagoon food web at that time (1974–1976). The study established that at Izembek Lagoon, the two primary carbon contributors were phytoplankton (for which particulate organic material or POM is a proxy) and eelgrass (*Zostera marina* L.), and that their $\delta^{13}C$ values were found to be sufficiently different so as to provide distinct carbon tracers throughout the food web. The study also found that eelgrass was a major source of carbon, especially to benthic organisms. Taxa with a higher reliance on phytoplankton were fish and epibenthic organisms (McConnaughey and McRoy 1979). This historic study was conducted before nitrogen stable isotope analysis was common, hence thus far, there are no isotope records showing trophic relationships in the Izembek eelgrass food web. Also, this historic study was completed before the onset of a shift in the Pacific Decadal Oscillation (circa 1977), a climatic event in the North Pacific that was shown to have significantly reorganized upper trophic levels <50 km away from the study site (Hare and Mantua 2000). Four decades after the 1970s study, the sub-arctic environment has undergone significant changes, including a decrease in sea ice thickness and duration (Mueter and Litzow 2008), increasing sea surface temperature, and northward species range shifts (Grebmeier 2012). These changes may be having impacts on the Izembek eelgrass food web. These impacts could have far reaching effects since Izembek provides nursery grounds for Bering Sea fisheries, and is a stopover for migratory waterfowl in the North American Pacific, East Asian-Australasian and West Pacific Flyways (Reed et al. 1989; U.S. Fish and Wildlife Service 1985).

The present study hypothesizes that due to regional changes in environmental conditions between the 1970's and 2008, there has been a shift in the food web at Izembek Lagoon toward a higher reliance on eelgrass-based carbon. This shift would present itself as an overall enrichment in the $\delta^{13}C$ values in organisms over time. To enhance our understanding of Izembek Lagoon's trophic architecture and to provide a baseline for future food web studies, nitrogen stable isotope compositions of organisms in the food web were also examined in this study. Overall, this study documents carbon and nitrogen stable isotope compositions that can be used for monitoring and for comparisons with other seagrass systems.

2.3 Methods

2.3.1 *Study Site*

Izembek Lagoon is situated 13 km north of Cold Bay, Alaska (55º14′40″N, 162º55′00″W) (Figure 2.1). Designated as a State Game Refuge, it covers 34,662 ha within the Izembek National Wildlife Refuge. The lagoon opens northwest to the Bering Sea, and is protected from storms by barrier islands. Salinity in the lagoon is between 26 and 32 (McRoy 1966). Eelgrass is the dominant aquatic vegetation (44–47% aerial coverage) in the lagoon, 83% of which is intermittently submerged by semidiurnal and mixed semidiurnal tides (Ward et al. 1997). Tidal range in the sampling area ranges from 0–1 m at low tide (Mean Low Low Water, MLLW).

2.3.2 *Sample Collection and Treatment*

Both quantitative and qualitative sampling was done using several methods across the lagoon to collect a representative sampling of organisms in the Izembek Lagoon food web. Systematic sampling of eelgrass, infaunal and epibenthic organisms was conducted at six historic stations along a transect that was established in the 1970s at Grant Point (McConnaughey and McRoy 1979; Figures 2.1 and 2.2). This transect was 900 m long and spanned 0–1.5 m water depth at MLLW. These historic stations were chosen to represent typical eelgrass zones in the lagoon: intertidal (3 stations), shallow subtidal (0–2 m; 2 stations), and subtidal (> 2 m; 1 station).

Epi- and infaunal organisms were sampled in 2008 within 3 m of each station with a 4 cm diameter PVC (polyvinyl chloride) core, similar to the historic study (McConnaughey and McRoy 1979). In 2008, three replicate cores were collected haphazardly at four of the stations (#1, 2, 3 and 4; Figure 2.2), however, due to logistical constraints, one station (#5) only had two replicates and a final station (#7) only had one. In the historic study, five to seven replicate cores were taken at each station. In 2008, cores were taken by carefully gathering eelgrass blades into the tube aperture, pressing it 10 cm into the sediment, and removing the entire column of substrate including seawater. Because of the infrequent occurrence of fauna (occasionally very large Nephtidae polychaetes) beyond 10 cm sediment depth in 1977 (McRoy, personal communication), core depth in 2008 was reduced to 10 cm to avoid much of the anoxic layer. In both studies, cores were placed in plastic bags, returned to the Cold Bay Fish and Wildlife field station laboratory, and either immediately sieved (1 mm mesh) with filtered seawater, or stored in refrigeration for up to three days until processing could occur. Epi- and infauna were sorted and identified to the lowest taxonomic level before being prepared for stable isotope analysis (described below).

Similar to the historic study, macroalgae (*Fucus gardneri, Ulva sp., Melanosiphon intestinalis)* were collected with the aforementioned core samples, but also opportunistically throughout the lagoon due to their low abundance within the cores. It was assumed from their low current and historic abundance (McConnaughey and McRoy 1979; Ward et al. 1997) that they were a less important food source compared with phytoplankton and eelgrass. Terrestrial sources of carbon were not sampled since the lagoon receives very low freshwater input from streams (McConnaughey and McRoy 1979). To account for variability in eelgrass density and morphology within and between stations on the transect, 1–10 eelgrass blades, roots, flowers and rhizomes were haphazardly collected from sediment cores at each station, homogenized, and run as single sample for stable isotope analysis. Samples of eelgrass blades were scraped free of epibiota (almost entirely epiphytic, single celled and filamentous algae) with a glass slide or paper towel. These epibiota were pooled to gain enough material (the total from four blades), homogenized, and run as single samples for stable isotope analysis as per the historic sampling protocol. Water-column particulate organic matter (POM) was used as an approximation of phytoplankton and was collected from 1–2 L seawater samples ($n = 15$) taken from several of Izembek's main tidal channels on an incoming tide. These were filtered through pre-combusted glass fiber (2.5 cm diameter, Gelman glass fiber AE) and visible inorganic particles and zooplankton were removed.

To access non-benthic organisms in the eelgrass food web, several different gear types were used and individuals were hand collected opportunistically. This qualitative collection strategy facilitated obtaining a representative sub-sample of mobile, ephemeral and patchy populations across Izembek Lagoon, and it adhered to the sampling strategy used in the 1970's by McConnaughey and McRoy (1979). Nekton and mobile epibenthic organisms were opportunistically hand-picked (e.g., *Telmessus cheiragonus* spotted during core sample collections and medusae taken en route to sample seawater) or seined (10 x 1.5 m beach seine with a 6.25 mm mesh size). Ten seine casts were conducted around Grant Point both on the transect and along the shoreline within 600 m of the transect to avoid sampling disturbance effects. Both patchy (non-continuous eelgrass turf; n = 2) and continuous turf (n = 3) vegetated beds were seined in 0–1.5 m of water. This occurred twice at each site (n = 10), once within two hours of low tide and once within two hours of high tide, to access a broad spectrum of eelgrass bed residents. Casts were taken from the water edge by dragging the net the full distance perpendicular to shore while care was taken to maintain substrate contact with the leadline and good flotation at the waters surface. After traversing in a half-moon configuration parallel to the shoreline, the net was gathered by hauling in the drawline to diminish volumn in the cod end. The cod-end's contents were poured into a bucket of seawater, sorted, and sampled onsite.

A 5 mm mesh hand-held push-net (0.5 m^2 opening) was deployed to target fast swimming organisms, which were unattainable in seine nets. Push-net swaths (10-15 m) were performed in the vicinity of the historic transect (Figure 2.2). Three swaths were intertidal and three were shallow subtidal (0–2 m). Swaths were sampled within two hours of low tide (+1 – -1.5 MLLW) by pushing the net forward into prevailing winds (generally southerly or south by south-westerly), which crossed the transect at a slight diagonal angle (Figure 2.2). This technique was adopted with the idea that pushing into surface currents from strong winds would counteract the net's forward pressure boundary, and may increase catch rate. Each swath was carried out within ≤ 1 hour of each other, and for this reason each were positioned at least 50 m apart to decrease the effect of sampling disturbance.

Nine fish traps (0.04 m^3 rigid-mesh) with a 5 cm conical one-way entrance were deployed haphazardly in subtidal areas (2–10 m depth at MLLW) around Grant Point. They were set at high tide (mean high high water, MHHW) to facilitate boat navigation through the lagoon's channel system. Traps were baited with frozen fish parts, weighted, bouyed, and placed in deep eelgrass beds several feet above or on the substrate to maximize access for cryptic eelgrass fauna. Traps were left out for a maximum of two tidal cycles due to low catch occurance and bad weather.

Fish and mobile invertebrates were sorted and euthanized with a CO_2 overdose (using ~5 AlkaSeltzer® tablets per five liters seawater) prior to laboratory processing. Bird tissue samples were obtained on loan from Izembek National Wildlife Refuge staff. Samples were immediately dried on a vacuum seal with silica gel for 24–36 hrs, or frozen at -20˚C, and then transported on dry ice. All tissues were freeze dried prior to stable isotope analysis. Organisms containing carbonate (e.g., *Evasterias sp., Turtonia sp.)* were soaked in 1 N hydrochloric acid (HCl) until fizzing ceased, rinsed with deionized (DI) water repeatedly until a neutral pH was reached and were then dried at 60°C. In organisms with adequate muscle tissue (fish, birds and some invertebrates), muscle tissue was used preferentially. Other organisms were processed as whole individuals, although some smaller organisms (e.g., *Boreocingula martyni, Caprella alaskana*.), were pooled as whole individuals to obtain the minimum amount of tissue required for stable isotope analysis. Dried tissues were homogenized unless otherwise noted. To account for variability in lipids content that have relatively lower $\delta^{13}C$ values compared with protein, carbon isotope values from samples were post-analytically corrected using a normalization method (McConnaughey and McRoy 1979, Sweeting et al. 2006). Carbon isotope values were also corrected for the historic decrease in $\delta^{13}C$ values of atmospheric carbon dioxide over time resulting from the Seuss effect, calculated as a total of -0.54‰ (0.0171‰ yr^{-1} from 1976 to 2008) (Bacastow et al. 1996). All $\delta^{13}C$ and $\delta^{15}N$ values of samples were determined using an elemental analyzer (EA) coupled on-line via a conflo-interface to an isotope–ratio mass spectrometer (ThermoElectron DeltaplusXP interfaced with a Costech ECS4010 EA) at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks. Analytical precisions for $\delta^{13}C$ and $\delta^{15}N$ analysis (expressed here as one standard deviation from multiple [n = 39] runs of peptone used as an internal standard) were ± 0.2‰ and ± 0.3‰ respectively. Stable carbon and nitrogen isotope ratios are expressed relative to international standards (Vienna Pee Dee Belemnite, or VPDB, for CO_2 and atmospheric nitrogen for N_2) and are reported in the conventional δ notation as per mil (‰) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000 \quad (1)$$

where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio C^{13}/C^{12} or $^{15}N/^{14}N$.

2.3.3 *$\delta^{13}C$ Mixing Model*

A two-source mixing model (McConnaughey 1978) was used to determine the proportional contribution of eelgrass and phytoplankton to consumers:

$$\%\ \text{eelgrass carbon} = (\delta`_p + I - \delta`_s / \delta`_p - \delta`_e) \times 100 \quad (2)$$

where subscripts p, s and e refer to phytoplankton, sample, and eelgrass, respectively. In this equation, '*I*' represents trophic fractionation, or the total increase in $^{13}C/^{12}C$ ratio occurring from preferential uptake of

^{12}C in metabolic processes along a food web pathway. Without testing the actual trophic fractionation at each step, it is impossible to create a mixing model with this equation. Thus, three scenarios were used that lay within published range of trophic fractionation factors (0.8 ± 1.1‰ per trophic level) (DeNiro and Epstein 1978). The three '*I*' values used were 0‰, 1.0‰, and 1.5‰.

2.3.4 *Statistical Analysis of Carbon Isotope Data*

Statistical tests were performed using Microsoft Excel 2003 Analysis ToolPak. Historic (1974–'76) and modern (2008) $\delta^{13}C$ values of organisms were compared using frequency histograms, regression analysis and one-way analysis of variance (ANOVA). In many cases, very few individuals of a species were collected from either time periods. Grouping organisms into coarse taxonomic status (usually to Class) and consumer category (e.g., filter feeder, detritivore, omnivore) created a larger sample pool. Even after grouping, some organisms had sample numbers too small for statistical tests (e.g., taxon groups unsegmented worms, limpets, medusae) or the isotope value was derived from a sample of many homogenized individuals (e.g., *Balanus sp., Halichondria panicea,* and *Turtonia sp.*). These are presented as an individual or pair-mean with no error bars. Other data are presented as group means (± 1 SD). In all cases, significance was accepted when $p \leq 0.05$, and discussed as potentially significant when $0.1 \leq P > 0.05$.

2.3.5 *Trophic Structure*

The $\delta^{15}N$ values of sampled taxa were used to determine trophic levels (TL) of the Izembek Lagoon food web. The model is based on an assumed +3.8‰ isotopic fractionation factor for nitrogen per TL (Hobson and Welch 1992). An average of eelgrass, eelgrass epibiota, and POM $\delta^{15}N$ values (6.2‰ ± 1.5) was used as a basis of primary production. Sequential trophic levels were calculated by adding 3.8‰ to this base, resulting in four trophic levels: TL1 = 6.2‰–10‰, TL2 = 10.1‰–13.9‰, TL3 = 14.0‰–17.8‰, TL4 = 17.9‰–21.6‰. Due to $\delta^{15}N$ variability in the sources of primary production (~1.5‰), there were rare occasions when an organism may have been assigned to two trophic levels. Decisions on final trophic level were made based on a literature review of the organisms' diet.

2.4. Results

2.4.1 *Temporal Carbon Comparison*

A frequency histogram of 24 exact species matches between 2008 and the mid 1970's shows that overall, modern organisms have shifted towards higher $\delta^{13}C$ values than those in the mid 1970's (Figure 2.3). Distribution of organisms in 2008 displays a peak of organisms with relatively higher $\delta^{13}C$ values, while a more even distribution marks 1974–'76 values. Higher $\delta^{13}C$ values (Table 2.1) correspond with more eelgrass-derived carbon (mean eelgrass signature in 2008: -10‰ ± 1.0, in 1974–'76: -9.8‰ ± 1.4) and lower values indicate a larger proportional contribution from POM (2008: -18.4 ± 1.5, in 1974–'76: -18.9 ± 1.4), a proxy for pelagic phytoplankton. When exact species matches were compared over the two periods using regression analysis, a positive relationship in $\delta^{13}C$ values was evident ($R^2 = 0.395$, $df = 21$) (Figure 2.4). No significant changes were found between the $\delta^{13}C$ values from POM ($P = 0.32$, $df = 33$), eelgrass blades ($P = 0.61$, $df = 26$) or roots ($P = 0.78$, $df = 11$) between time periods.

Significant increases in $\delta^{13}C$ values were evident from benthic biota in 2008 relative to the 1970's values (Table 2.2). When grouped into broad taxonomic categories (Figure 2.5), polychaetes ($P < 0.01$, $df = 23$), shrimp ($P < 0.01$, $df = 8$) and unsegmented worms ($P < 0.01$, $df = 6$) showed a significant increase (at $\alpha = 0.05$) in $\delta^{13}C$ values in 2008 relative to their 1970's values. Additionally, clams ($P < 0.1$, $df = 6$), and limpets ($P < 0.07$, $df = 3$) had significantly higher $\delta^{13}C$ values at $\alpha = 0.1$. No significance was calculated for sponges because individuals were pooled in both years ($df = 1$); however, an increase in $\delta^{13}C$ values of 5.28‰ from historic values was noted in 2008 organisms. When the organisms were grouped by consumer categories (Figure 2.6), five of the seven category means showed an increase in $\delta^{13}C$ values (benthic predator, deposit feeder, invertebrate grazer, filter feeder). Of these, significant differences were evident for detritivores ($P < 0.01$, $df = 43$), deposit feeders ($P < 0.01$, $df = 6$) and filter feeders ($P = 0.02$, $df = 10$).

2.4.2 *$\delta^{13}C$ Mixing Model*

Of the ten species with exact matches from the two sampling periods, all but three (*Evasterias troschelii, Telmessus cheiragonus* and *Hexagrammos stelleri*) showed an increase in the proportional contribution of eelgrass in their diet (Table 2.3). Slightly increased consumption (<10%) of eelgrass-derived organic matter occurred in four organisms, four showed increases between 10–20%, and one had a >50% increase over historic values. Percent increases were constant regardless of the trophic fractionation variable ('*I*'). However, as '*I*' increased, the mixing equation returned values of over and fewer than 100% for total carbon input, reflecting limited usefulness of the model. This likely reflects a mis-assignment in the model of carbon sources in these organisms diets, an error that is magnified as '*I*' increases. Misidentified portions of dietary carbon could include end-members from terrestrial sources, epiphytic algae (eelgrass epibiota), or macroalgae, none of which were included in this two-source model.

2.4.3 *Trophic Structure*

Izembek Lagoon's two main primary producers (Table 2.1) were significantly different from each other in terms of $\delta^{13}C$ values (one-way ANOVA, $P < 0.01$, $df = 42$) but not in $\delta^{15}N$ values ($P = 0.27$, $df = 42$). In 2008, POM $\delta^{13}C$ values ranged between -22.0 and -16.6‰ (mean-18.4‰) and between 3.0 and 7.3‰ (mean 5.8‰) for $\delta^{15}N$ values. Eelgrass $\delta^{13}C$ values ranged between -11.9 and -6.8‰ (mean -10.0‰) and between 1.0 and 11.8‰ (mean 6.3‰) for $\delta^{15}N$ values. Eelgrass $\delta^{13}C$ values were less variable than POM (SD ± 1.0 vs. ± 1.5, respectively), but eelgrass $\delta^{15}N$ values were more variable than POM (SD ± 1.7 and SD ± 1.1, respectively). The $\delta^{15}N$ values of sampled taxa (Table 2.1) were used to determine trophic levels of the Izembek Lagoon food web, shown as a stepwise increase (+3.8‰) in $\delta^{15}N$ values over the averaged food source (Figure 2.7). Beginning with an average $\delta^{15}N$ value of 6.2‰ at the primary-producer level, this food web apparently has four trophic levels. Most resident first-level trophic organisms were infaunal deposit feeders (e.g., *Abarenicola pacifica,* maldanid and orbiniid polychaetes), epibenthic detritivores (e.g., *Microjassa sp.*) and non-specific omnivores (e.g., *Anisogammarus sp., Margarites helicinus, Littorina sitkana*) or non-specific grazers (*Boreocingula martini, Anisogammarus sp.*). Trophic level 1 also represented the majority of the birds sampled. The second trophic level represented the greatest diversity of resident fauna, and was represented by deposit feeders (e.g., polynoid polychaetes, *Harmothoe imbricata, Golfingia sp.*), a few detritivores (e.g., *Caprella alaskana, Holmesiella anomala*), a variety of non-specific benthic grazers (e.g., *Tectura persona, Idotea sp., Nucella canaliculata*), water column predator fish (*Oncorhynchus nerka, Microcottus sellaris, Hexagrammos stelleri* and *Ammodytes hexapterus*) and benthic predators (*Evasterias troscheli, Gasterosteus aculeatus*). The majority of the third level trophic organisms were fish (e.g., *Pallasina barbata, Platichthys stellatus*) and bird scavengers (*Larus spp*.). Scavengers from two phyla occupied the fourth trophic level (*Orchestoidea sp.*, *Larus glaucescens*, *Larus canus brachyrhynchus*).

2.5 Discussion

The isotopic evidence presented here indicates that much of the food web of Izembek Lagoon has shifted to a higher reliance on eelgrass-derived carbon since the 1970s. Unlike traditional analysis of diet metrics such as gut content analysis, $\delta^{13}C$ values show food assimilation over long periods of time, averaging the variability of an individual's diet. Animal emigration and immigration can be a confounding factor in food web studies based on stable isotope data. Both undefined carbon sources and time limitations for the integration of food items into tissues can present problems when interpreting an organism's stable isotopic values. This was not considered a problem here because these results focused on species known to be lagoon residents. Past studies have grouped individuals into taxonomic guilds for the purpose of examining group responses to various perturbations such as natural variability in environmental parameters (Roth and Wilson 1998; Koulouri et al. 2006), habitat modification (Schlosser 1982), pollution effects (Gaston et al. 1998; Mistri et al. 2000; Mirto et al. 2002), dredging (Morello et al. 2005; Chabanet et al. 2010), and bottom trawling (Garrison and Link 2000). This technique is based on an assumption that broad taxonomic groupings have similar characteristics, such as morphometrics, life history, metabolic demands, and mobility. In this study, taxonomic guilds helped to clarify the significant role of mobility. Temporal differences in carbon partitioning were seen in taxa with limited mobility such as sponges, unsegmented worms, polychaetes, clams, and limpets (Figure 2.5). These organisms are sessile or have low mobility and therefore a somewhat restricted diet of locally produced water column food. They also are heavily reliant on the detrital food web, which is the primary fate of unexported eelgrass. An additional dimension of carbon partitioning within a food web is the mechanism by which food is processed and assimilated by organisms. Feeding mechanisms are thought to be of primary importance to the structuring of marine ecosystems (Pearson and Rosenberg 1987), and grouping organisms by consumer categories has been successful in defining functional redundancy and impacts in fisheries after disturbance (Kaiser et al. 2006; Auster and Link 2009), functional responses in benthic systems (Bremner et al. 2003; Cosentino and Giacobbe 2008), and habitat partitioning (Gladfelter and Johnson 1983; Moens and Vincx 1997). When organisms were grouped into feeding categories, those showing significant increases in eelgrass carbon were filter feeders, detritivores, and deposit feeders (Figure 2.6). One explanation for the shift to a greater reliance on eelgrass-derived carbon is that there is greater availability of eelgrass detritus now than in the mid 1970's. Greater availability would show up first in the benthic realm where it is bacterially processed and introduced into the food web via detritivores, deposit and filter feeders. Although recent estimates of eelgrass biomass are limited, spatial coverage of eelgrass within the lagoon has been periodically documented, showing a small increase (~6%) between 1978 and 1987, and < 1% increase from 1987–1995 (Ward et al. 1997).

Two important abiotic conditions have changed from the historic 1974–1976 study that may have influenced eelgrass productivity: cloud cover and temperature. Biomass production of eelgrass is mainly regulated by irradiance, temperature and nutrients (Phillips et al. 1983; Dennison et al. 1993; Lee et al. 2007). Atmospheric data from Izembeck's closest weather stations (Cold Bay, 13 km to the south and St. Paul, 515 km to the northwest) show a decrease in overcast days in the growing season since the mid 1970's (Angeloff 2011). *In situ* and lab experiments on *Zostera spp*. suggest irradiance, especially at temperate, light limited latitudes, is a limiting factor for shoot growth and vegetative expansion (Dennison et al. 1993; Ochieng et al. 2010), with increasing irradiance positively affecting shoot biomass and survival (Olesen and Sand-Jensen 1993; Short et al. 1995). Although irradiance usually co-varies with temperature, many studies suggest temperature is the primary factor controlling seasonal growth of seagrass (Phillips et al. 1983; Bulthuis 1987; Dunton 1994). At Cold Bay and St. Paul, rising temperatures in spring and autumn have increased the potential growing season so that more days fall within 15–20ºC, the optimal growth temperature of eelgrass (Lee et al. 2005). In particular, over the forty-four year air temperature record at Cold Bay, mean monthly averages for February have risen above the freezing temperature of seawater (2000–2008: -0.55°C, 1990–1999: -2.45°C, 1980–1989: -1.98°C, 1974–1979: -3.25°C), increasing the chance of shore-fast ice breakup early in the spring (Angeloff 2011). Other studies have shown that general warming trends in the Bering Sea have caused a decrease in thickness and duration of sea ice (Mueter and Litzow 2008), which inhibits early spring eelgrass growth in shallow nearshore areas by limiting light (McRoy 1969).

If a trend of increasing reliance on eelgrass continues at Izembek Lagoon, then secondary production may increase in organisms that can capitalize on eelgrass detritus (Hader et al. 2011). The exact effects of a shift toward increased eelgrass in the Izembek food web are unknown because the majority of documented shifts in primary production elsewhere have been toward increased macroalgae via eutrophication (Douglass et al. 2011; Olsen et al. 2011) and not towards eelgrass, as seen in Izembek Lagoon. However, regime shifts in other ecosystems have shown that a change in primary production can have marked influences on higher trophic levels (Gunderson 2001; Viaroli et al. 2008; Jiao 2009). One case-study is the well-documented Florida Bay ecosystem, which transitioned from clear water-seagrass dominated to turbid-phytoplankton bloom dominated in the mid-1980's (Gunderson 2001). It is postulated that the loss of mega-grazers (e.g., manatee, sea turtles) and fisheries (e.g., spiny lobster) was caused by the shift in dominant primary producers (Butler et al. 1995; Fourqurean and Robblee 1999). On the other hand, changes in abundance of key organisms can pose top-down pressure on seagrass populations (Baden et al. 2012), also causing regime shifts that favor competing primary producers. This scenario is more likely at Izembek where shifts in primary production may give competitive advantage to detritus, deposit and possibly filter feeders; organisms that directly benefit from eelgrass detritus. These groups represent the majority of organisms in the first through second trophic levels at Izembek, and significant faunal reorganization in these levels may spur changes in the current balance of food web interactions (e.g., predation, grazing, benthic organic sediment processing). Food web reorganization has proven consequential in Sweden where overfishing played a significant role in the loss of seagrass ecosystems (Baden et al. 2012). There, depletion of the cod fishery caused an overabundance of their primary prey, predators on meso-grazers. The subsequent loss of meso-grazers caused increased abundance of fouling seagrass epiphytes which, along with increases in mean water temperature and eutrophication, caused seagrass declines upward of 60% in just two decades (Pihl et al. 2006). This cascade of losses has been blamed for reductions in gross fishing income of 8–11 million (U.S.) dollars yr^{-1} and over 110 thousand dollars yr^{-1} in private and municipal beach maintenance costs (Troell et al. 2005). Another example of economic losses around eelgrass beds due to food web reorganization comes from Chesapeake Bay. Its associated eelgrass ecosystem supported a commercial fishery with annual landings exceeding 225,000 metric tons until the mid-1990's when landings declined to around 170,000 tons (Houde et al. 1999). Among other anthropogenic factors causing fishery decline (Kemp et al. 2005), thermal stress has been implicated in eelgrass die-off, depopulating the area of nursery and forage habitat for fish and invertebrates (Moore and Jarvis 2008). Other areas of concern for eelgrass health are increased fresh water input from spring precipitation, high-temperature related hypoxia, and an increase in salinity variability due to both temperature and changed fresh water flow (Najjar et al. 2010). Ecological impacts to Cheseapeake Bay's eelgrass, the foundation of this ecosystem, have had reverberating effects throughout its associated food web that has led to declines in important regional fisheries.

Since the eelgrass bed at Izembek Lagoon is essential nursery habitat for many ecologically and economically important species in the adjacent Bering Sea, food web reorganization here could mean similar losses to fisheries and ecosystem services (Deutsch et al. 2003; Walker et al. 2010). A study in Chesapeake Bay suggests that, to a certain extent, benthic grazers, detritivores and other mid-level trophic organisms exhibit a large degree of diet plasticity and may maintain stable populations with small production shifts (Douglass et al. 2011). However, it has also been widely documented that seagrass systems show drastic changes in biodiversity and abundance of mid-level trophic consumers with increased and continued perturbation (Dennison et al. 1993; Lee et al. 2007), in turn altering use patterns in higher level consumers (Deegan 2002). For a pristine system such as Izembek Lagoon, this likely means continued stability in mid-level trophic positions if the trend of small changes over the scale of decades continues. However, accumulated stressors to an ecosystem over time can wear down its resiliency, enabling even small shifts, such as primary production fluctuations or trophic interactions, to cause regime change (Hauxwell et al. 2003; Folke et al. 2004; Pihl et al. 2006). Small shifts at Izembek could be the first signs of a larger trend. These baseline data will help to clarify what role food web reorganization will play in this, and other sub-arctic nearshore ecosystems.

This work contributes a new dimension for future ecosystem studies at Izembek Lagoon by providing baseline $\delta^{15}N$ values and suggesting a trophic architecture for eastern Bering Sea seagrass ecosystems. Previous food web studies have been described in soft-bottom estuarine lagoons in the Beaufort Sea where major inputs are from pelagic production and terrestrial carbon (Dunton et al. 2012). In these higher latitude systems, seasonality and shorefast ice cover play even larger roles than at Izembek Lagoon. Similar to Izembek Lagoon, the coastal Beaufort Sea lagoons contained up to four trophic levels, which were dominated by omnivorous detritivores dependent on microbial processing. Similarly, Izembek Lagoon's greatest species diversity was represented in mid-level consumers, which rely on seagrass detritus and the microbial loop. At Izembek, resident organisms in the first (e.g., *Anisogammarus sp*., *Margarites helicinus*, *Littorina sitkana*, maldanid and orbiniid polychaetes) and second levels (e.g., *Turtonia minuta*, *Sipunculidae*, *Caprella alaskana*, polynoid polychaetes) inhabit the benthic and epibenthic realm where eelgrass provides stable substrate and many habitat niches. Predatory benthic fish also occupy trophic level two, capitalizing on the same habitat niches as foraging space. Microbial processing of terrestrial- (Dunton et al. 2012) and seagrass-based carbon was a critical step for carbon enrichment in upper trophic levels for both these studies. This implies that benthic organisms directly connected with the microbial loop should be monitored for change as they are a key link in the energy transfer to upper trophic levels.

2.6 Conclusion

Using stable carbon and nitrogen isotopes, this study assessed the importance of current primary producers within the Izembek Lagoon food web and tested this food web for changes against the one assessed during the mid-1970's. Izembek Lagoon lacks direct human disturbances; however, the food web still shows signs of change. This study suggests change was induced by increases in eelgrass carbon, possibly caused by increases in temperature and irradiance in the region. Results from nitrogen stable isotope analysis also formed a baseline for trophic architecture of the Izembek Lagoon food web, and displayed the bulk of organisms within trophic levels two and three. Documenting the unique stable isotope values of organisms is a critical first step to gaining insight on how and when food webs transition under changing conditions. This baseline will be instrumental in monitoring for larger, long-term alterations and understanding how even pristine seagrass systems are affected by environmental drivers.

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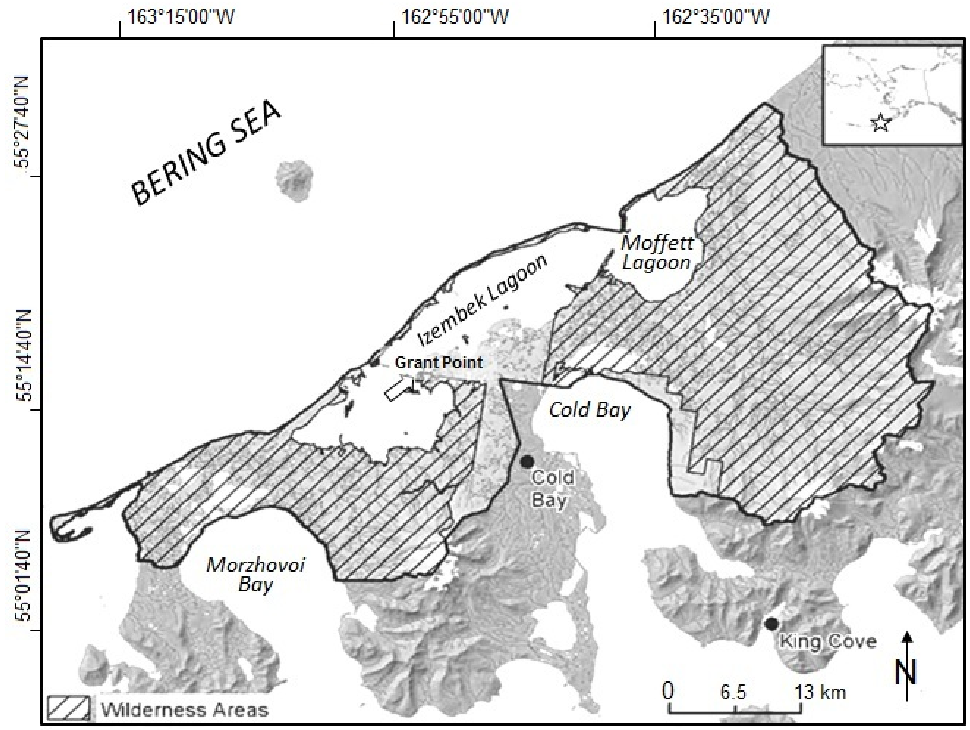

Fig 2.1 Izembek Lagoon and surrounding wilderness area (hatch pattern), Alaska Peninsula, U.S.A. Arrow shows approximate location of Grant Point historic transect

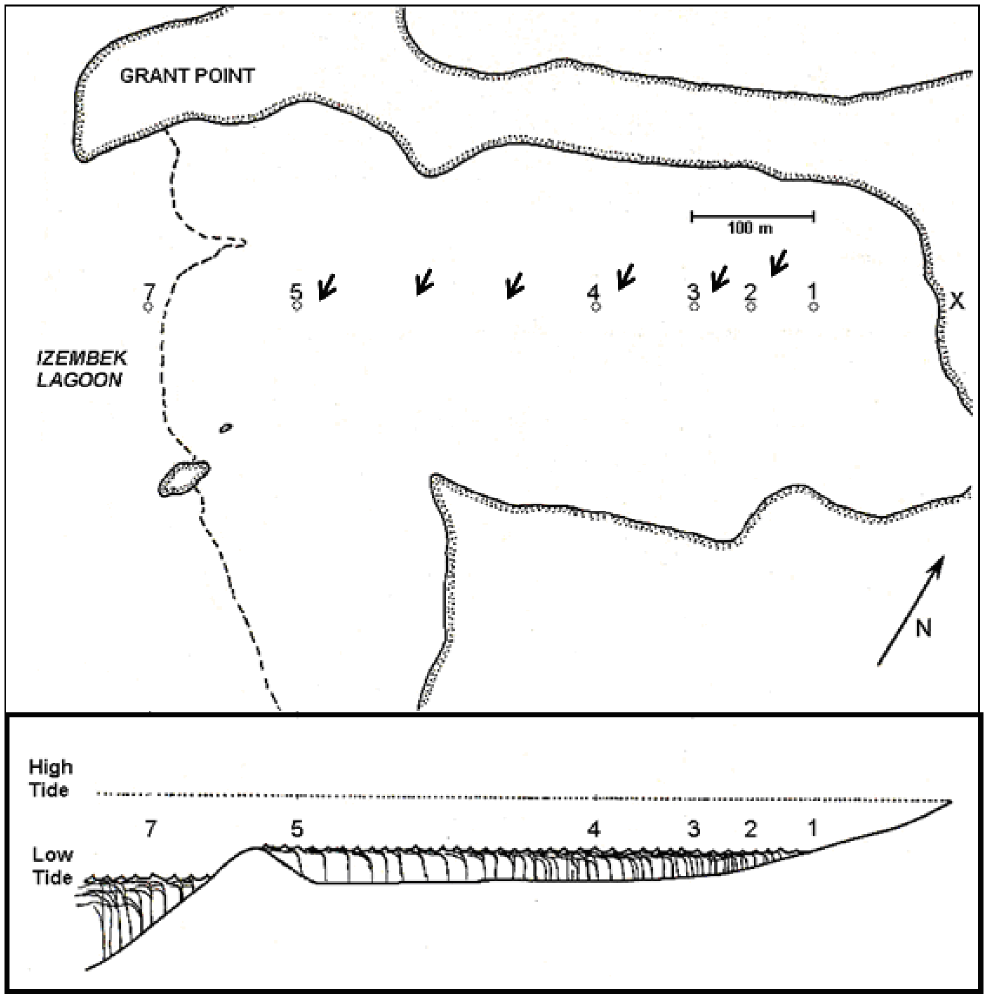

Fig 2.2 Sampling transect at Grant Point showing relative depth strata. Numbers represent stations in 1974–'76 and 2008. Arrows show the approximate locations of push-net swaths. The transect begins with a permanent boulder (X) on the beach and becomes progressively deeper along an intertidal bench (extent demarked with dashed line), ending at subtidal station 7

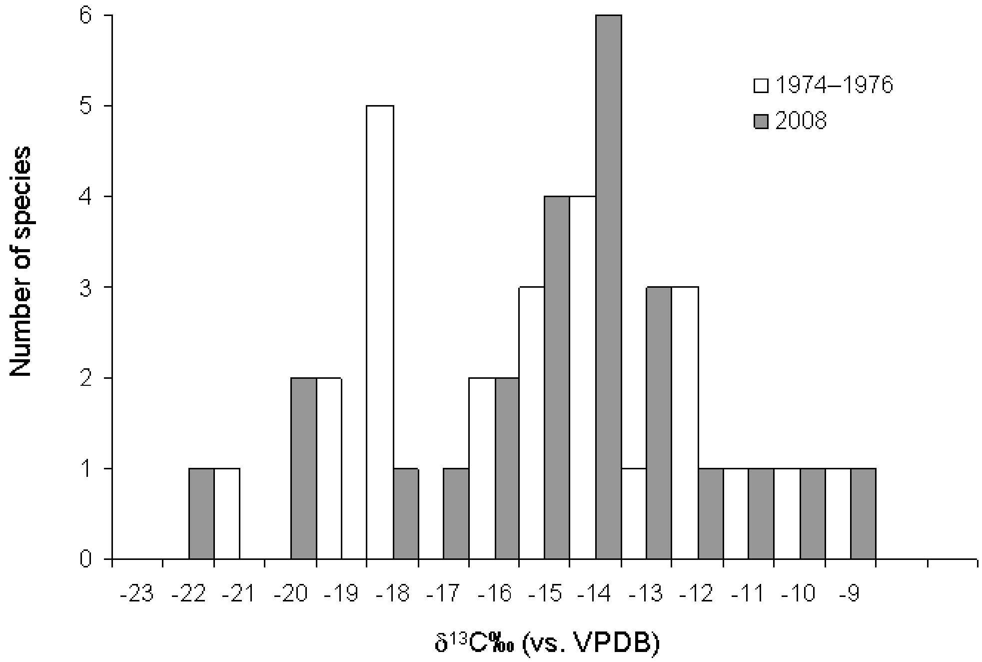

Fig 2.3 The frequency distribution of historic and modern $\delta^{13}C$ values in 24 benthic species from the Izembek Lagoon food web, Alaska

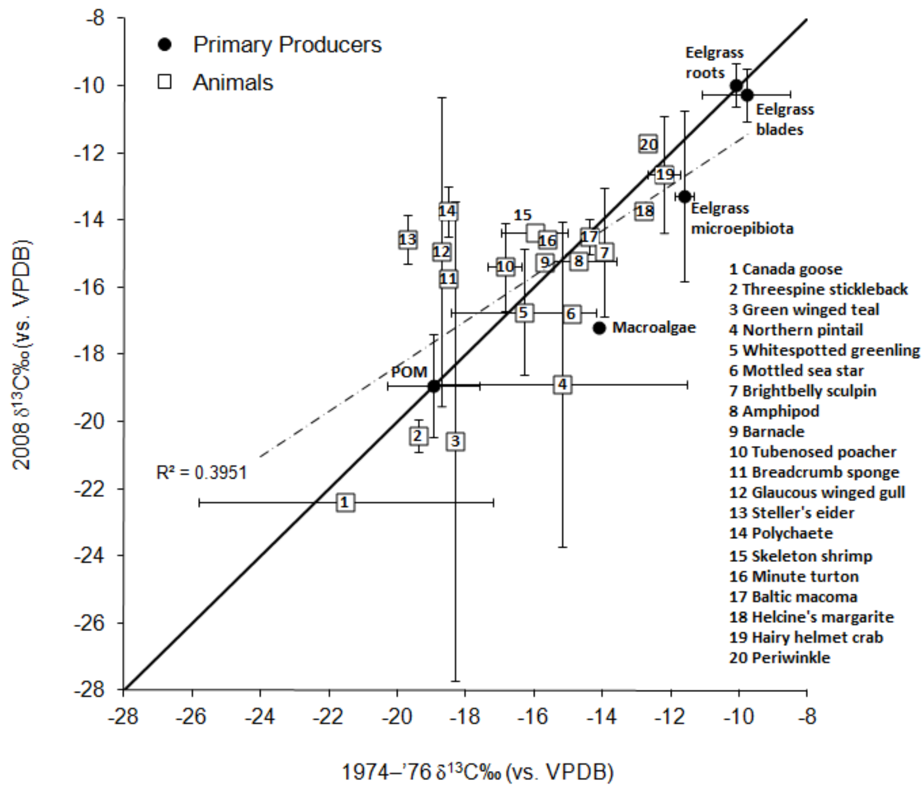

Fig 2.4 Linear regression of δ^{13}C values from historic and modern lipid normalized tissues (dotted line, $R^2 = 0.3951$). Deviation from $R^2 = 1$ (solid line) confirms changes in δ^{13}C values of 21 species, POM and epibiota from the Izembek Lagoon food web. Error bars show one standard deviation

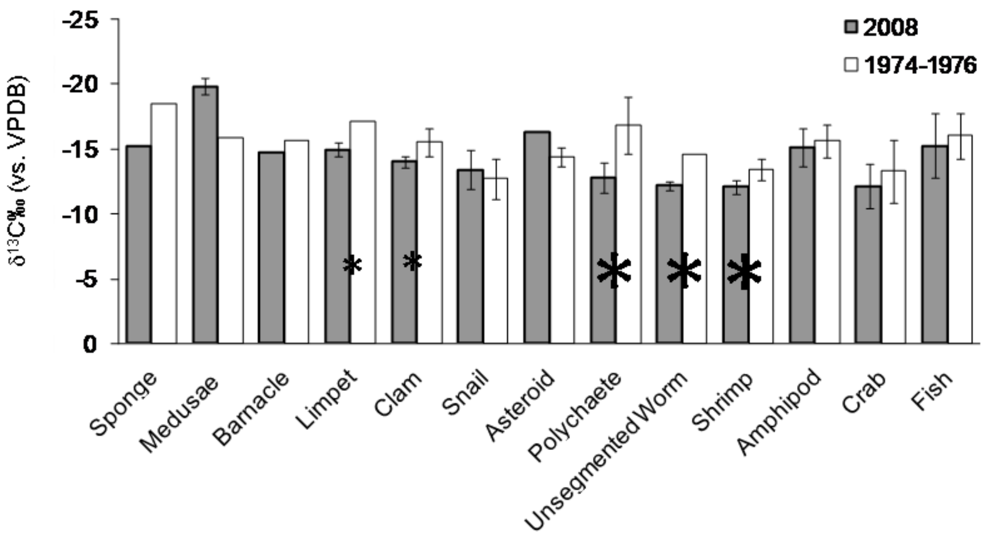

Fig 2.5 Mean $\delta^{13}C$ values (± 1 SD) of grouped taxa in 1974 –'76 and 2008. A large asterisk (*) denotes significant ($P \leq 0.05$) differences between years. A small asterisk (*) denotes less significant differences ($P \leq 0.1$) between years. Significance and standard deviation bars are not reported for taxa with n <3. Values have been lipid normalized and the Seuss effect has been taken into account.

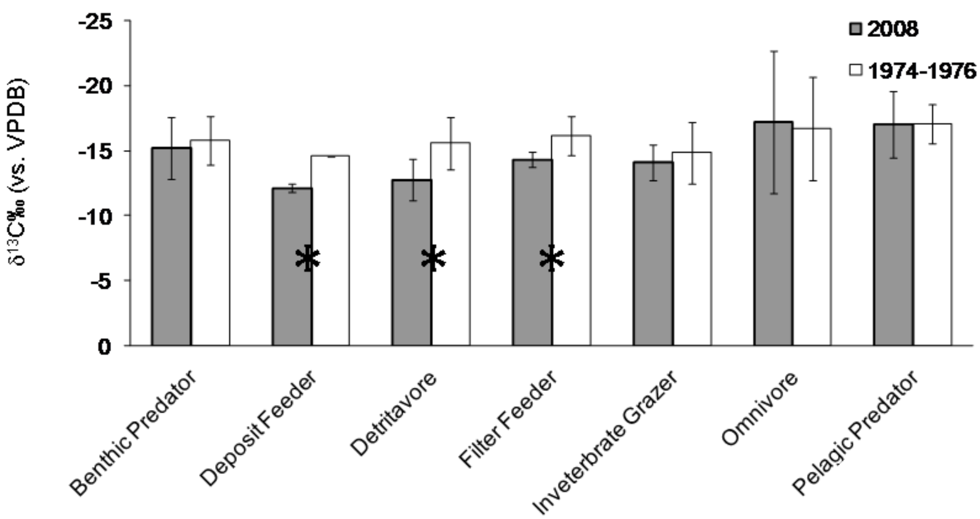

Fig 2.6. Mean $\delta^{13}C$ values (± 1 SD) of organisms grouped by consumer category in 1974 –'76 and 2008. An asterisk (*) denotes significant differences ($P \leq 0.05$) between years. Values have been lipid normalized and the Seuss effect has been taken into account.

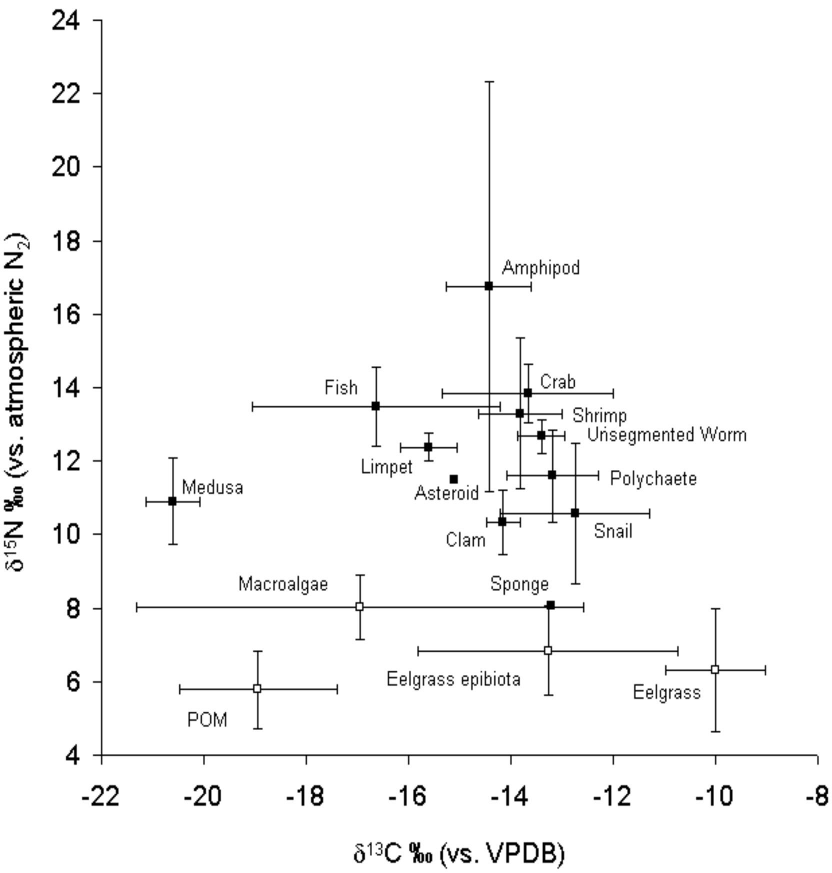

Fig 2.7 Stable carbon and nitrogen isotope values for primary producers (open box), and fauna (closed box) from 2008 shown as taxonomic categories. Error bars denote one standard deviation (SD) within taxonomic group. Values have been corrected for the Seuss effect and all but non-fatty tissues (cellulose) have been lipid normalized.

Table 2.1 Mean δ^{13}C values (² 1 SD) of primary producers in 2008 and 1974 –’76. All samples were homogenized for isotope sampling, and several individuals were pooled for each sample in 2008. Sample numbers (n) reflect the total number of individuals

	Sample Description	**1974–'76** δ^{13}**C‰ (± 1 SD)**	**(n)**	**2008** δ^{13}**C‰ (± 1 SD)**	**(n)**
Macroalgae					
	Acrosipohonia sp.			-20.7	(1)
	Fucus gardneri	-14.1	(1)	-16.7	(1)
	Melanosiphon intestinalis			-12.0	(1)
	Chorda filum	-14.3	(1)		
Microalgae					
	Microepibiota	-11.4 & -11.8	(2)	-12.8 ± 2.5	(4)
Eelgrass					
	Zostera marina, flowers			-6.3	(1)
	Zostera marina, leaves	-9.8 ± 1.3	(5)	-9.6 ± 0.9	(57)
	Zostera marina, rhizomes			-9.3 ± 0.7	(10)
	Zostera marina, roots	-10.1	(1)	-9.9 ± 0.7	(59)
	Zostera marina, all samples	-9.8 ± 1.2	(6)	-10 ± 1.0	(136)
POM					
	Seawater particulates filtered on incoming tide	-18.9 ± 1.4	(19)	-18.4 ± 1.5	(15)

Table 2.2 Stable isotopic values (δ^{13}C and δ^{15}N) of organisms collected from Izembek Lagoon eelgrass ecosystem presented as (n) replicates with standard deviations (² 1 SD). Values were lipid-normalized for non-feather tissues, and the Seuss effect was accounted for in 2008 samples. When lipid normalization was not possible, values are shown in bold. Sample values were from individual specimens (I) or pooled specimens (P). Two values for a single specimen denote two separate isotope analyses for one specimen. Tissues were homogenized as whole bodies (H), muscle (M), feather (F), fat (T), gonad (G), or skin (S)

Sample Description		**1974–1976 ‘δ^{13}C‰ (± SD)**	**(n)**		**2008 ‘δ^{13}C‰ (± SD)**	**2008 δ^{15}N‰ (± SD)**	**(n)**
Arthropoda (Crabs, Shrimp, etc.)							
Anisogammarus sp. (Amphipod)	I H	-13.6 & -15.8	(2)	I H	-13.4	10	(1)
Balanus glandula (Barnacle)	P H	**-15.7**	(1)	P H	-14.7	11	(1)
Caprella alaskana (Amphipod)	P H	-14.7 & -16.4	(2)	P H	-13.8	13	(1)
Caridea (Shrimp. sp. #1)				I M	-13.7	14	(1)
Caridea (Shrimp. sp. #2)				I M	-13.7 & -13	14 & 14.0	(1)
Caridea (Shrimp sp. #3)				I M	-14.6	15	(1)
Coelopa frigida (Beach wrack fly)				P H	-8.4	12	(1)
Calliopius laeviusculus (Amphipod)	I H	**-14.5**	(1)				
Ampithoe sp. (Amphipod)	I H	**-12.4**	(1)				
Metopella nasuta (Amphipod)	I H	**-17.6**	(1)				
Oradarea sp. (Amphipod)	I H	**-14.7**	(1)				
Holmesiella anomala (Shrimp)				I M	-13.1	14	(1)
Idotea sp. (Isopod)				P H	-13.5	14	(1)
Microjassa sp. (Shrimp)				I M	-15.0	9.2	(1)
Orchestoidea sp. (Isopod)				P H	-15.0	21	(1)
Heptacarpus camtschatica (Shrimp)	I H	**-12.4** & **-13.0**	(2)				
Telmessus cheiragonus (Hairy helmet crab)	I M	13.0 ± 0.5	(2)	I M	-13.7 ± 1.7	14 ± 0.8	(3)
Pagurus hirsutiusculus (Hermit Crab)	I H	**-17.6**	(1)				
Aves (Birds)							
Anas acuta (Northern pintail)	I L	**-12.6**	(1)	I F	**-21.0** ± 5.6	8.4 ± 3.4	(8)
Anas acuta	I M	**-17.8**	(1)	I M	-20.8 ± 5.2	8.2 ± 2.5	
Anas americana (American widgeon)				I M	-19.0 ± 2.4	6.4 ± 1.2	(4)
Anas americana				I F	**-21.1** ± 3.7	6.1 ± 1.1	
Anas carolinensis (Green winged teal)				I F	**-16.2** ± 4.7	10 ± 3.5	(9)
Anas carolinensis	I M	**-18.3**	(1)	I M	-20.1 ± 5.3	8.6 ± 2.6	
Anas platyrhynchos (Mallard)				I F	**-17.2** ± 6.8	7.3 ± 3.5	(5)
Anas platyrhynchos				I M	-17.3 ± 5	7.5 ± 3.2	
Branta bernicla (Black brant)				I T	-12.4		(1)
Branta bernicla				I M	-18.7 ± 4.2	7.5 ± 1.4	(17)
Branta bernicla				I F	**-18.9** ± 5.9	7.3 ± 3.0	(9)
Branta canadensis (Canada goose)	I M	**-22.9** ± **2.6**	(3)	I M	-21.4	4.8	(1)
Branta canadensis	I L	**-24.2** & **-14.6**	(2)				
Cygnus columbianus (Tundra swan)				I F		5.0	(1)

Table 2.2 Continued

Sample Description		**1974–1976 δ^{13}C‰ (± 1 SD)**	**(n)**		**2008 δ^{13}C‰ (± 1 SD)**	**2008 δ^{15}N‰ (± 1 SD)**	**(n)**
Aves continued							
Larus canus brachyrhynchus (Mew gull)				I F		16.3	(1)
Larus glaucescens (Glaucous gull)	I M	**-18.7**	(1)	I F	-18.9 ± 0.4	16.1 ± 0.1	(50)
Larus glaucescens	I T	**-16.2**	(1)				
Polysticta stelleri (Steller's eider)	I M	**-19.7**	(1)	I F	-15.8 ± 0.6	15.3 ± 0.5	(10)
Philacte canagica (Emperor goose)	I M	**-17.0**	(1)				
Calidris sp. (Sandpiper)	I M	**-20.8**	(1)				
Cnidaria (Jellies)							
Gonionemus vertens	I H	**-15.9**	(1)				
Cyanea capillata				I G	-21.0	10.7	(1)
Cyanea capillata				I H	-20.2	11.8	
Echinodermata (Sea stars)							
Leptasterias sp.	I H	**-13.9**	(1)				
Evasterias troschelii	I H	-13.7	(1)	P H	-15.1	11.5	(1)
Mollusca (Gastropods and Bivalves)							
Acmaea testudinalis (Limpet)	I H	**-17.1**	(1)				
Boreocingula martyni (Snail)				P H	-13.9 ± 0.1	9.0 ± 0.2	(1)
Lacuna variegata (Snail)	I H	-9.9	(1)				
Littorina sitkana (Snail)	I H	-11.5	(1)	P H	-10.4	10.7	(1)
Lottia digitalis (Limpet)				I M	-15.0	12.0	(2)
Macoma balthica (Clam)	I H	-13.5	(1)	I M	-14.3 ± 0.3	9.9 ± 0.3	(3)
Margarites helicinus (Snail)	I H	-12.5	(1)	P M	-12.1	10.4	(1)
Mya arenaria (Clam)	I H	-15.4	(1)				
Nucella canaliculata (Snail)				I M	-13.5	13.7	(4)
Tectura persona (Limpet)				P M	-15.8	12.8	(1)
Thais lamellosa (Snail)	I H	**-14.6**	(1)				
Turtonia minuta (Minute turon)	I H	-15.3	(1)	P H	-13.8	11.6	(1)
Unk. Limpet				P M		12.4	(1)
Osteichthyes (Bony Fish)							
Ammodytes hexapterus (Sandlance)				I M	-19.0	12.3	(1)
Gasterosteus aculeatus (Threespine stickleback)	I M	-19.8	(1)	P M	-21.2 & -21.3	12.2 & 11.6	(1)
Hexagrammos octogrammus (Masked greenling)	I M	-15.4	(1)				
Hexagrammos stelleri (Whitespotted greenling)	I M	-15.2	(1)	I M	-17.0 & -16.8	12.7 & 12.4	(2)
Hippoglossus stenolepis (Pacific halibut)	I M	-17.8	(1)				
Lepidopsetta bilineata (Rock sole)	I M	-14.8	(1)				
Microcottus sellaris (Brightbelly sculpin)	I M	**-14.0 ± 0.2**	(3)	I M	-16.1 ± 2.2	14.1 ± 0.7	(3)
Myoxocephalus polyacanth-ocephalus (Great sculpin)	I M	-13.7	(1)				
Oncorhynchus nerka (Sockeye salmon)				P M	-16.4	13.3	(1)
Pallasina barbata (Tubenose poacher)	I M	-17.5	(1)	I M	-16.3 ± 1.3	14.6 ± 0.7	(2)
Pholis laeta (Crescent gunnel)	I M	-14.0	(1)				
Platichthys stellatus (Starry flounder)				I M	-15.0 & -14.7	15.0 & 14.5	(2)

Table 2.2 Continued

Sample Description		1974–1976 '$\delta^{13}C$‰ (± 1 SD)	(n)		2008 '$\delta^{13}C$‰ (± 1 SD)	2008 $\delta^{15}N$‰ (± 1 SD)	(n)
Osteichthyes continued							
Pungitius pungitius (Ninespine stickleback)	I M	**-19.1**	(1)				
Theragra chalcogramma (Alaska pollock)	I M	-15.4	(1)				
Unk. fish #1				I M	-15.5	13.7	(1)
Unk. fish #2				I M	-14.3& -13.5	13.5 & 13.3	(1)
Polychaeta (Bristle worms)							
Abarenicola pacifica				P H	-14.4± 0.1	9.1 ± 0.1	(3)
Arenicola glacialis	I H	-15.9	(1)				
Eteone longa				P H	-12.9± 0.4	12.5 ± 0.3	(3)
Haploscoloplos sp.	PH	**-20.4** & **-20.4**	(2)				
Harmothoe imbricata				P H	-13.1± 0.4	13.0 ± 0.5	(4)
Maldanidae				P H	-13.8± 0.9	10.7 ± 0.1	(3)
Nephtys caeca	I H	-16.3	(1)				
Orbiniidae				P H	-13.2± 0.1	10.8 ± 0.4	(3)
Rhynochospio sp.	PH	**-17.6**	(1)				
Polynoidae				P H	-11.7± 0.4	12.4	(3)
Porifera (Sponges)							
Halichondria panicea	I H	-17.7	(1)	P H	-13.2	8.1	(1)
Unsegmented Worms							
Echiurus echiurus (Spoon worm)	I H	-15.3	(1)				
Sipunculida (Peanut worm)				I S	-13.2± 0.3	12.6 ± 0.3	(4)
Golfingia (Peanut worm)				P H	-13.1	13.4	(1)
Nemertea #1 (Ribbon worm)				I H	-14.1	12.4	(1)
Nemertea #2 (Ribbon worm)				I H	-14.2	12.5	(1)
Nemertea #3 (Ribbon worm)				I H	-13.3	12.7	(1)

Table 2.3 Mixing model results of carbon partitioning in the organisms of Izembek Lagoon showing three levels of possible trophic level fractionation and an organism's corresponding reliance on eelgrass carbon (%). Bold numbers indicate the animal(s) compared have more complex carbon sources than the mixing model could account for within the given trophic fractionation level. Overall percentage shifts to eelgrass with negative numbers indicate a higher reliance on POM between the two time periods while positive values indicate a higher reliance on eelgrass.

Trophic level fractionation		0		1		1.5		
Species	**Shift to eelgrass**	**1974–'76**	**2008**	**1974–'76**	**2008**	**1974–'76**	**2008**	**(n)**
Hexagrammos stelleri	-19%	40	21	18	**-1**	7	**-12**	1, 2
Evasterias troschelii	-14%	57	43	35	21	24	9	1, 1
Telmessus cheiragonus	-6%	65	59	42	37	31	25	2, 3
Margarites helicinis	+6%	70	76	59	65	54	59	1, 1
Anisogammarus sp.	+7%	55	62	44	51	38	45	2, 1
Littorina sitkana	+14%	81	95	70	84	65	78	1, 1
Pallasina barbata	+15%	15	30	**-8**	**8**	**-19**	**-3**	3, 2
Caprella alaskana	+17%	40	57	18	35	7	23	2, 1
Turtonia minuta	+19%	39	58	17	36	6	25	1, 1
Halichondria panicea	+52%	12	64	1	53	**-4**	**47**	1, 1

Chapter 3: Temporal comparison reveals a shift in the benthic eelgrass (*Zostera marina* L.) community from 1977 compared to 2008 at Izembek Lagoon, Alaska[1]

3.1 Abstract

Seagrass ecosystems harbor diverse infaunal and epifaunal communities. Biodiversity and density changes in seagrass faunal communities could influence higher trophic level organisms that rely on benthic foraging within these ecosystems. Benthic community diversity and density associated with the seagrass bed at Izembek Lagoon, Alaska were compared between 2008 and historical data collected in 1977. While various biodiversity measures (e.g., Shannon-Wiener diversity, Margalef's richness, and taxonomic distinctness) appeared stable over time, overall organism density was higher in 2008 compared to 1977. Individual species increased up to 77-fold per m^2 since 1977, depending on the species. Bivalves (*Turtonia sp., Macoma balthica*) and gastropods (*Boreocingula martyni*, *Littorina sitkana*) were primarily responsible for this increase in epibenthic invertebrates. This change in density may have been caused by shifting eelgrass morphology, such as an increase in leaf area, in response to local environmental changes (e.g., increased irradiance and temperature). This study shows that significant faunal community reorganization has occurred in this seagrass ecosystem, and identifies environmental shifts as possible drivers of this change.

[1] Tippery, A. C. Temporal comparison reveals a shift in the benthic eelgrass (*Zostera marina* L.) community from 1977 compared to 2008 at Izembek Lagoon, Alaska. Prepared for submission to 'Estuaries and Coasts

3.2 Introduction

Worldwide efforts to quantify the effects of changing environmental conditions on seagrass systems have been prompted because of the importance of seagrass functions and the ecosystem services they provide. These changing conditions include sea-level rise, ocean acidification, increased frequency of catastrophic storms, and elevated temperatures (Seddon et al. 2000; Scavia et al. 2002; Orth et al. 2006). Seagrasses evolved from terrestrial origins into the marine realm during the Cretaceous period, an epoch with warmer and more acidic oceans than the present (Berner 1991). Though it is expected that they will adapt to, and possibly thrive in present-day oceans with lower pH (Beer and Koch 1996), our understanding of the impact of environmental changes is lacking in high-latitude seagrass systems at the edge of their temperature and irradiance tolerance thresholds (Short and Neckles 1999; Wassmann et al. 2011).

Izembek Lagoon, (55º14′40″N, 162º55′00″W Alaska U.S.A), a shallow embayment of the Bering Sea, is an ecologically important sub-arctic seagrass bed within the protected Izembek National Wildlife Refuge. It is a prime candidate for monitoring climate effects on seagrass ecosystems without confounding anthropogenic stressors like coastal development and pollution due to the pristine nature of the bed (Sowl and Poetter 2004), its protected status, and global wildlife importance (International Union for Conservation of Nature and Ramsar Convention 1987). Nevertheless, despite its remote location, Izembek Lagoon is likely affected by climate alterations such as warming temperatures, reduced ice cover, and increased ocean acidification. Already, regional climate changes such as the Bering Sea ice retreat (Mueter and Litzow 2008) and shifting storm patterns (Ward et al. 2008) have been linked to regional community-wide distribution shifts of fish, invertebrates and birds with increases in total biomass and species richness. However, repercussions, if any, to the ecologically and economically important Izembek Lagoon or other subarctic seagrass ecosystems have not been quantified.

Seagrasses are considered foundation species in that their presence alters the environment around them. Like other marine foundation species (e.g., coral reefs and kelp beds), seagrasses are long lived (Larkum and den Hartog 1989; Ruggiero et al. 2002) and provide multiple ecosystem functions. These include habitat creation (Heck et al. 2003), nutrient cycling (de Boer 2007), water quality maintenance (Koch et al. 2006), and low energy boundary layer formation at the seafloor, which enhances sediment settlement processes (Reusch and Chapman 1995). Seagrass leaves, roots and rhizomes produce structural complexity that is highly correlated with increased species biodiversity compared to un-vegetated surrounding areas (Heck and Orth 1980; Lazzari 2002; Gullström et al. 2008). Leaves extend into the water, providing three-dimensional refugia for small demersal fishes and invertebrates (Lazzari 2002; Heck et al. 2003; Koch et al. 2006), and an increase in the availability of substrate for encrusting organisms like bryozoans, coralline and filamentous or single celled algae and their associated grazers (Leliaert et al. 2001). Thick mats of rhizomes on and in surface sediments provide additional substrate for physical attachment for bryozoans (Cocito et al. 2012) and refuge from physical forces present in the intertidal zone (Fonseca et al. 1983; Koch 2001). Roots and rhizomes also act as a conduit for oxygen into anaerobic sediments supporting microbial and fungal communities, which facilitate nutrient and energy transformation (Blum and Mills 1991; Viaroli et al. 1996). The biodiversity supported by structural components of seagrasses subsequently facilitates production in the ecosystem (Duarte 2000).

Much of seagrass ecosystem production is carried out by the benthic community, in part due to resource partitioning involved in nutrient transformation (Karlson et al. 2010). The basic processes of decomposition by shredders and detritivores (Peduzzi and Herndl 1991; Newell 1993), nutrient transport by bioturbators and filter feeders (Lopez and Levinton 1987; Norkko and Shumway 2011), and nutrient transformation and cycling by microbes (Newell 1996; Holmer and Bachmann-Olsen 2002), all take place in the benthos. The key process of organic load consumption within bottom sediments is positively correlated with seagrass grazer diversity and abundance. This demonstrates the important role that benthic biodiversity plays in energy transfer (Stoner 1980a; Canuel et al. 2007). The specific roles of benthic dwellers and their importance to ecosystem processes are reasonably well understood (Snelgrove et al. 1997). In contrast, we do not understand how changes in diversity and abundance of benthic organisms could affect those same ecosystem processes. It has, however, been suggested that shifts in benthic community biodiversity and abundance will impact the functions and processes in both seagrass beds and adjacent marine and terrestrial environments (Levin et al. 2001).

A result of carbon transformation by benthic communities in seagrass habitats can be increased biodiversity in higher trophic levels (Heck et al. 2008). Macrofaunal populations are a primary food source for fin fishes, large mobile invertebrates (Johnson and Thedinga 2005), waterfowl (Bustnes et al. 2000), and even some terrestrial organisms (Taylor and Sowl 2008). For example, fat reserves gained by waterfowl that spend time feeding in seagrass beds subsequently fuel their flights from northern breeding to southern wintering grounds (Hansen and Nelson 1957; Ganter 2000). Motile benthic foragers also act as vectors, exporting biomass and energy generated in the seagrass benthos to other marine realms (Levin et al. 2001; Heck et al. 2008). The benthic community at Izembek supports economically important Bering Sea fisheries species including Pacific halibut (*Hippoglossus stenolepis*), Pacific cod (*Gadus macrocephalus*), sandlance (*Ammodytes hexapterus*), and all five species of Pacific salmon (*Oncorhynchus keta, O. tshawytscha, O. gorbuscha*, *O. kisutch, O. nerka*) (Alaska Department of Fish and Game 2010). It also is critical foraging habitat for harbor seals (*Phoca vitulina*) and northern sea otters (*Enhydra lutris kenyoni*) that make daily migrations from adjacent pelagic habitats (Alaska Department of Fish and Game 2010).

Finally, isolated benthic habitats such as Izembek Lagoon will likely increase in proportional importance for migratory birds as other staging areas along the Pacific Flyway (e.g., Puget Sound, Willapa Bay, and San Francisco Bay) become more urbanized (Moore et al. 2004).

The aim of this study was to survey the benthic community structure (diversity and density) at Izembek Lagoon in 2008 and compare these data with a previous benthic survey conducted in 1977. Given that local weather patterns have become more favorable for eelgrass growth over the past 40 years (Angeloff 2011), and anecdotal evidence from elsewhere suggests that eelgrass at this location is becoming more foliose, which positively influences the benthos (Edgar 1990; Edgar and Robertson 1992; Lee et al. 2001), the expected results of this study are for increased biodiversity and density of benthic fauna from 1977 to 2008.

3.3 Methods

3.3.1 *Study Site*

Izembek Lagoon (55º14′40″N, 162º55′00″W), located in Izembek National Wildlife Refuge, Alaska, is the largest continuous (34,662 ha) and one of the most northern seagrass beds in the world (McRoy 1966, Barsdate et al. 1974) (Figure 3.1). Semi-diurnal and mixed tides inundate 83% of the lagoon (mean tidal range, 1 m), of which 78% are tidal flats and 22% are channels (Taylor and Sowl 2008). Eelgrass (*Zostera marina* L.) is the dominant aquatic vegetation in the lagoon, with 44–47% aerial coverage (Ward et al. 1997). In the 1970's, eelgrass densities were high with up to 5,000 shoots m^{-2} (McRoy 1970). The standing crop was last estimated at 4.6 x 10^5 metric tons in August 1964 (McRoy 1966; Barsdate et al. 1974). Opening northwest to the Bering Sea, Izembek Lagoon is protected from seasonal storms by barrier islands. Salinity varies from 26 to 32, but is lower to the northeast (McRoy 1966) due to freshwater input from the Joshua Green River, which drains into the adjoining Moffet Lagoon (Figure 3.1).

3.3.2 *Sampling Design*

Random sampling across the entire Izembek Lagoon was hampered by unpredictable weather, dangerous tides and impractical boat access. Therefore, a permanent 900 m transect was established south of Grant Point (Figures 3.1 and 3.2) in 1974 at the beginning of the 1970s study conducted by McConnaughy (1978). This area and transect line were chosen because they represent the full range of eelgrass bed depth strata and proximity to typical features such as shore and tidal channels. For the present study, six permanent stations were sampled along the original transect, representing typical eelgrass zones in the lagoon: three intertidal, two shallow subtidal (0–2 m), and one subtidal (> 2 m) (Figure 3.2). Five of these stations were sampled in the historic study and a sixth (station 5) was added in 2008 to augment the intertidal station 4, which is at a comparable depth. Light intensity decreases quickly with depth, therefore, various depth strata were chosen because light is the main driver of eelgrass morphology (Hemminga and Duarte 2000) and productivity (Nelson and Waaland 1997).

Stations were sampled between June 22nd to July 5th 2008 for eelgrass and benthic organisms. At each station, three replicate 0.0217 m^2 cores were haphazardly placed within 3 m of the transect and inserted 10 cm into the sediment (up to and frequently past anoxic sediments). Two stations had fewer core samples taken (station 5 had two cores and station 7 had one). Cores were removed, bagged, and either processed at the Cold Bay Fish and Wildlife field station laboratory, or preserved in formalin and returned to the laboratory at the University of Alaska Fairbanks for processing. In the laboratory, cores were sieved over a 1 mm mesh, organisms were identified to lowest taxonomic level possible using Banse and Hobson (1974) Hobson and Banse (1981), and Kozloff (1987), and then enumerated. The permanent transect was first sampled from July 24th to August 3rd 1977 (McConnaughey 1978), when five to seven 0.0214 m^2 cores were haphazardly sampled to a sediment depth of 20 cm within 3 m of each station. Because of the infrequent occurrence of fauna (occasionally very large Nephtidae polychaetes) beyond 10 cm sediment depth in 1977, core depth in 2008 was reduced to 10 cm after initial coring efforts to avoid much of the anoxic layer (McRoy, personal communication). Where possible, voucher specimens of uncertain identification were confirmed by University of Alaska Fairbanks taxonomists (Nora Foster, Max Hoberg).

3.3.3 *Comparison of Data Sets*

Due to minor differences in volumes of sediment sampled in 1977 vs. 2008 (0.0214 vs. 0.0217 m^2) and differences in the numbers of replicates and stations sampled, several steps were taken to test comparability between the 1977 and 2008 data sets. The additional core depth in 1977 did not greatly contribute to organism density (McRoy, personal communication); therefore, samples were converted to density (individuals per m^2) and considered comparable between years. Sampling effort plays a considerable role in biodiversity assessments. Generally, the number of species accumulates with increasing area sampled until true population richness is reached (Ugland et al. 2003). The 1977 data set had an average of five replicates per station, compared with three replicates per station in 2008. To test whether decreasing replicates changed the community assessment of diversity and density, a proxy 1977 data set was created (subsequently referred to as 1977*) by randomly choosing three replicates from the full 1977 data set. This 1977* data set was compared to the 2008 data set in addition to the full 1977 data set.

To test the null hypothesis that 1977, 1977* and 2008 benthic communities were not significantly different in diversity and density, ordination of samples by multi-dimensional scaling (MDS) overlain with cluster analysis and analysis of similarity (ANOSIM; Primer-E v6) one-way crossed pair-wise tests between year groups were performed (Clarke and Gorley 2001). Stations were analyzed for similarities between 1977, 1977* and 2008 using both tests based on a resemblance matrix with species as variables and average faunal core density/station as samples. A Bray-Curtis coefficient was used and the sample statistic significance level was $\alpha = 0.2\%$. Data were log (x + 1) transformed before analysis to increased the effect of rare species. Non-parametric tests were chosen because of the non-uniform nature of abundance data where most of the variables (species presence) within a sample are typically zero. For the ANOSIM test, an R statistic approaching 0 indicates similarities between and within groups are approximately the same. An R statistic approaching 1 indicates all replicates within the group were more similar to each other than any replicates from different groups.

Diversity indices were calculated with Primer-E v6 software for the 1977, 1977* and 2008 data, which were then compared between years using a one-way analysis of variance (ANOVA; Excel Office Pro 2003). Significance was set at $\alpha = 0.05$. Various diversity index measures (Pielou's evenness, Shannon-Wiener diversity, and Margalef's richness) were compared between years at the species level. This was possible because taxa were given unique identifications (e.g., polychaete 1), although they could not always be identified with corresponding genus and species. Average taxonomic distinctness (Δ^+) was therefore calculated on the taxonomic class level. Where class was unknown, phylum was used. Taxonomic distinctness is based on standard Linnaean classification in which each branch of the taxonomic tree is assigned an equal distance (Clarke and Gorley 2001). Average taxonomic distinctness measures the average distance of each taxon pair in a presence/absence species list of each year being compared. This statistic is largely independent of sampling effort and densities and is representative of phylogenetic diversity in a sample (Clarke and Warwick 1998). To understand which taxa were responsible for changes in composition between years, a BEST match test was conducted on the taxonomic class level using log (x + 1) transformation, Spearman rank correlation, stepwise testing with 99 random starts and limiting the output to one and five best matches at the taxonomic level of class (where rho >0.95). The BEST analysis allows for the bias inherent in a selection of variables from one matrix (years) to explain the patterns in the second (taxonomic variation).

3.4 Results

There was considerable overlap in the community data between1977 and 1977*, indicating no differences in community composition based on density as a result of rarifying the data sets (Figure 3.3). The null hypothesis of no differences in community composition (species and density) between 1977 and 1977* was confirmed using ANOSIM testing, but significant differences existed between 2008 and both versions of the 1977 data set (Table 3.1). Diversity indices were also compared between 1977 and 1977* and no significant differences were detected using one-way ANOVA tests (Table 3.2). As 1977 and 1977* density-based data sets were not significantly different, direct comparisons between 2008 and 1977 data sets were completed for all other tests (Appendices 1.1, 1.2).

Diversity indices revealed no significant change in the benthic community between 1977 and 2008 (Table 3.2, Appendices 1.1, 1.2), except for Pielou's index, which showed that the overall community was more equitably distributed in 1977 than in 2008 ($P = 0.01$, $df = 41$; Table 3.2, Figure 3.4). Although Pielou's metric is related to Shannon-Wiener biodiversity, the lower evenness in 2008 was not enough to create significant differences between the mean Shannon-Wiener biodiversity score ($P = 0.62$, $df = 41$; Table 3.2, Figure 3.5). Margelef's index (Figure 3.6) had not changed significantly between 1977 and 2008 ($P = 0.25$, $df = 41$; Table 3.2), nor did average taxonomic distinctness (Δ^+) exhibit significant differences between the two years ($P = 0.73$, $df = 41$; Table 3.2).

Organism densities in 2008 were significantly higher ($P \leq 0.01$, $df = 41$; Table 3.2, Figure 3.7) than in 1977, and bivalves were found to be primarily responsible for this increase (Figure 3.8). Based on mean number of individuals per m^2 in core samples, this taxon was ~77 times more abundant in 2008 than in 1977, representing 48.1% of the total change in density between these two years (Figure 3.9). Gastropods had the second largest increase (13-fold) from 1977 to 2008, and represented 32.8% of the total change in density between years. Polychaetes only increased 1.4-fold from 1977 compared to 2008, representing 4% of total change in individual densities between the two time periods. When restricted to one response variable, BEST tests showed the taxonomic group responsible for 80.8% of this change was the bivalves (Table 3.3). Test runs restricting output to five response variables accounted for a total of 86.0% of the change over time due to bivalves, gastropods, malacostracans, polychaetes, and priapulids (Table 3.3).

3.5 Discussion

Knowledge of how northern seagrass systems react under changing environmental pressures is crucial to developing predictive mitigation tactics for our coastal resources (Duarte 2002; Boudouresque et al. 2009). The important contribution of this study was to assess and isolate changes in a sub-arctic seagrass benthic community over a 40-year period, and offer possible explanations for these changes based on long-term environmental data (i.e., average cloud cover and temperature, Angeloff 2011). Results from this study at Izembek Lagoon have broad implications for general northern latitude seagrass systems facing similar challenges related to changing environmental conditions. This is because a hallmark of all seagrass ecosystems is that many of the critical functions they provide (e.g., nutrient transformation, carbon processing) are orchestrated by the same specific activities of benthic organisms. Though no two seagrass ecosystems have identical species assemblages, those organisms that are present fall into functional groupings (e.g., detritivores, bioturbators, deposit feeders), which are similar across latitudes and regions (Levin et al. 2001). Changes in benthic community distribution (e.g., species diversity, evenness, organism density) can depopulate or over populate these functional groups, disrupting the services that they provide (Levin et al. 2001), including support of higher trophic levels within and external to the seagrass bed (Duarte 2000). Increasingly, seagrass system alterations occur as synergistic effects from direct human manipulations (e.g., nutrient loading, coastal development, overfishing; Short et al. 1996) and climate change (e.g., temperature stress, increased irradiance, ocean acidification; Short and Neckles 1999; Hale et al. 2011). These alterations include community-wide redistributions to which the benthic community is particularly susceptible (Afli et al. 2008; Per-Olav et al. 2008), which is why monitoring changes in the benthos is important for assessing the overall ecosystem.

Many of the ecosystem functions associated with seagrass beds are executed by specific activities of benthic organisms, emphasizing the importance of species diversity and community distribution (Levin et al. 2001). Overall, some taxa in Izembek's benthic community were more abundant in 2008 compared to 1977, but the community was similar in both years in terms of species composition and diversity, with the exception of a less evenly distributed (Pielou's index) modern species assemblage. No significant differences were seen in biodiversity (Shannon-Wiener index), species richness (Margalef's index) or taxonomic distinctness (Δ^+) between years. It is possible, though unlikely, that changes in evenness were caused by slight differences in sampling methodology. For example, the end of sampling in 2008 occurred 19 days prior to the beginning of the sampling period in 1977. Small seasonal differences in sampling period between the two years may have played a role in abundance of colonizing epiphytes (e.g., spionid polychaetes, coralline algae, and bryozoans), which can reach very high concentrations on eelgrass leaves prior to leaf senescence, at which point epiphytes enter the detrital pool. Epiphytes are grazed by epifauna (e.g., *Boreocingula martyni*) and eventually add to infaunal production after leaf shed (Hemminga and Duarte 2000; James et al. 2009). Benthic communities are well coupled to food quality and quantity, and temporal variability in food availability can quickly change benthic diversity and abundance (Montagna et al. 1983; Danovaro and Gambi 2002). Eelgrass leaves have around a 55 day growth period before senescence in more southern temperate systems like Puget Sound (Nelson and Waaland 1997). In a shorter sub-arctic growing season, several weeks of unaccounted colonization time could have a significant outcome on epiphytic densities that contribute to epifaunal density. In addition to small seasonal differences, differences in sampling effort between the two years may have affected the results. For example, echiuroids occurred in 1977 but did not appear in the 2008 samples. Absence of echiuroids in 2008, compared to < 100 m^{-2} in 1977, could be a relic of lower sampling effort in 2008 rather than a true absence in the benthos. However, these taxa make up only a small fraction of individuals in the community assemblage, and played only a small role in changes in evenness and density between 1977 and 2008.

Epibenthic bivalves in particular, and to lesser extent gastropods, were more abundant in 2008 compared with 1977. The reasons for this are unclear, but changes in eelgrass morphology, such as an increase in leaf surface area, could better facilitate feeding habits of the main species that increased in density in 2008. Abundance and diversity of benthic invertebrates are often correlated with structural complexity in seagrass beds (Hily and Bouteille 1999; Talley et al. 2000; Carvalho et al. 2006). Leaf surface area of eelgrass can positively influence epifaunal density and diversity, more so than leaf length and shoot density alone (Sirota and Hovel 2006). Seagrass plants with a greater surface area per unit weight (more foliose) can provide more protection for organisms than plants with smaller leaves (Heck and Orth 1980; Stoner 1980b). Comparison of leaf morphology on the historic transect between 2002/03 and 1978 suggests that eelgrass plants had more leaves in 2002/03, but less biomass (i.e., higher surface area per leaf; McRoy and Wendling, unpublished data). *Turtonia sp.* and *Boreocingula martyni* were the taxa that increased most in density over the two time periods. *Turtonia sp*. are bivalve filter feeders (Kafanov and Chepiga 1980) that access the water column by attaching to positively buoyant eelgrass leaves. This positions them in higher currents than experienced on the seafloor. *Boreocingula martyni* are non-discriminate gastropod grazers that also inhabit eelgrass leaves, feeding on epiphytic algae, colonial organisms and debris particles (Waren 1996). If eelgrass plants were becoming more foliose in Izembek Lagoon, it would provide increased grazing area for *B. martyni* and additional leaves for water column ingress to *Turtonia sp*.

A survey of seagrass standing stock and leaf morphology across the lagoon would be needed to determine if eelgrass plants were more foliose in 2008 compared to 1977. However, four decades of local weather data (1974–2008) show trends that would support these morphological changes. An overall 1.09°C increase in air temperature during the spring growing season (February–April) over these 34 years in Izembek Lagoon (Angeloff 2011) has brought the modern ambient air temperature above the freezing point of sea water. This is occurring as early as February (2000–2008 February mean: -0.55°C) compared to colder air temperatures that supported shorefast sea ice in the latter 1970's (1974–1979 February mean: -3.25°C). As a proxy for sea surface temperature in Izembek Lagoon's shallow waters, warmer air temperatures could mean early loss of shore-fast ice. Concurrent cloud cover data show average decreases in overcast skies throughout the growing season (decrease between 1974–1979 vs. 2000–2008) March–May 5.0%, June–Aug. 1.27%, Sept.–Nov. 5.07%; Angeloff 2011). This has resulted in an increase in irradiance and extension of the ice-free growing season, both positive factors for seagrass production (Lee et al. 2007). However, the effects of abiotic changes are not always straightforward. More available irradiance and an extended ice-free growing season at this location also benefit competing macroalgae and phytoplankton (Zaldivar et al. 2009). Increases in light and temperature, with concurrent increased nutrient loading **(**Burkholder et al. 2007) have been shown to give advantage to floating producers over rooted vascular producers such as seagrass (Scheffer et al. 2003). Though an unlikely scenario in pristine areas like Izembek Lagoon with no anthropogenic nutrient inputs, this synergy of stressors has previously caused regime shifts in other seagrass dominated systems (Hauxwell et al. 2003; Troell et al. 2005; Zaldivar et al. 2009).

From the perspective of the last forty years, higher benthic invertebrate density may indicate elevated carrying capacity of the seagrass system for benthic grazers and their associated predators. For example, this may benefit migratory birds whose last stop for reliable invertebrate forage and refuge before trans-ocean migrations is Izembek Lagoon (Tibbits et al. 1996). Steller's Eiders (*Polysticta stelleri*) are one of the 31 species of shorebirds and many more migrants relying on this habitat, and are a good representative of fauna at high trophic levels whose futures depend on benthic level production. This is due to their use of seagrass beds during flightless molt periods, when they forage on benthic bivalves, amphipods, small gastropods, bivalves and crustaceans (Bustnes and Systad 2001a, b; Systad and Bustnes 2001; Wang et al. 2010). Additionally, Steller's Eiders exhibit high fidelity to molting sites (Bowman and Brown 1992), and possibly their dependence on the benthic community at Izembek Lagoon is due to low environmental variability and consistency of habitat found there (Flint et al. 2000). Steller's Eiders have been in global decline since the 1960's and were listed in 1997 as threatened under the Endangered Species Act (U.S. 50 CFR Part 17a). Izembek and neighboring Nelson Lagoon are two of the most important molting and staging sites for the entire Pacific Steller's Eiders population (Petersen 1981; Dau et al. 2000) because the benthic forage satisfies their high nutritional demands as feathers are replaced and calories are stored for migration (Petersen 1981). Increased benthic production also means better forage for marine mammals. Sea otter populations in the Bering Sea differ from nearshore sea otters elsewhere in that the shallow continental shelf allows a larger and more pelagic (up to 50 km offshore) range while foraging for benthic invertebrates (Taylor and Sowl 2008). However, Izembek State Game Refuge Management Plan (Alaska Department of Fish and Game 2010) suggests that northern sea otters (*Enhydra lutris kenyoni*) are now concentrating more in the sheltered lagoons and bays of Izembek National Wildlife Refuge than in previous decades (Taylor and Sowl 2008). Izembek's northern sea otter population is listed as threatened under the Endangered Species Act. The U.S. Fish and Wildlife Service is currently considering designating nearshore waters, including Izembek Lagoon, as critical habitat for this species (U.S. 50 CFR part 17b). The benthic helmet crab (*Telmessus cheiragonus*) is abundant in Izembek Lagoon and is an important food source for sea otters in that area (McConnaughey 1978, Alaska Department of Fish and Game 2010).

Among many other lagoon residents, harbor seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubatus*), and spectacled eiders (*Somateria fischeri*) are species of concern who may benefit from increased benthic production forage in the eelgrass of Izembek Lagoon.

Over future decades or possibly centuries, a higher carrying capacity based on high abundance of calcifying organisms, such as the bivalves and gastropods found in increased densities in this study, could weaken the food web links explained above. Ocean acidification increases seagrass production (Palacios and Zimmerman 2007), which supports the benthic community. However, this benefit comes at the detriment of calcareous benthic residents (Hall-Spencer et al. 2008). Ocean acidification raises serious concerns for marine calcifiers because the rate of calcification is directly related to seawater carbonate saturation (Langdon et al. 2000; Dupont et al. 2008; Andersson et al. 2009). Weakened skeletons and reduced growth and development of various marine invertebrates have been documented in both larval and adult stages under decreasing pH levels (Raven et al. 2005; Dupont et al. 2010). Examples in temperate waters include the mussel *Mytilus edulis* and the Pacific oyster *Crassostrea gigas*, which are declining with increasing partial pressure of dissolved CO_2 in seawater under levels predicted by the Intergovernmental Panel on Climate Change for 2100 (Gazeau et al. 2007). Organisms potentially affected by lowered seawater pH at Izembek Lagoon include bivalves, gastropods, coralline algae, calcifying crustaceans, and polychaetes with calcareous tubes. Of these, bivalves and gastropods have increased significantly in density since the 1970's, and are important taxa supporting higher trophic levels. Because of its relatively cold water, ocean acidification in the North Pacific is expected to impact marine calcifiers on a scale of decades (Andersson et al. 2008), which is likely an insufficient amount of time to allow higher trophic level species to adapt their foraging strategies to changing prey species. While seagrasses themselves are expected to benefit from ocean acidification due to the increased soluble CO_2 available for photosynthesis (Zimmerman et al. 1997; Palacios and Zimmerman 2007), lower ocean pH is not expected to benefit competing marine primary producers. Studies have shown no significant effect on macroalgae, which are already carbon saturated in present day conditions (Beer and Koch 1996). For coccolithophores (Zondervan 2007), and dinoflagellates (Rost et al. 2006), increasing CO_2 concentration means decreasing calcification, which may or may not be balanced out by concurrent positive effects of increased photosynthesis. Seagrasses may gain a competitive edge because lower pH may help deplete calcareous epiphytic growth that shades seagrass canopies. Conversely, it could also deplete invertebrate mesograzers, which keep fouling epiphytes in check (Hall-Spencer et al. 2008; Martin et al. 2008). Losses of this nature at Izembek's eelgrass beds could devalue the lagoon as critical habitat.

Given the role of benthic organisms in nutrient processing and transfer, climate shifts are drivers for losses or gains in diversity. Mechanistically, benthic organism abundance could either directly or indirectly reduce or increase overall secondary production in seagrass beds (Levin et al. 2001; Hale et al. 2011). Anthropogenic-mediated losses of seagrass-associated benthic diversity are a common scenario worldwide. Eutrophication is a common force of benthic reorganization that causes upward trophic losses (Peterson et al. 1994; Gonzalez-Oreja and Saiz-Salinas 1999) and has depleted local food web diversity at all trophic levels in Florida Bay, Florida (Hunt and Nuttle 2007; Fourqurean and Robblee 1999) and Waquoit Bay, Massachusetts (Fox et al. 2010). Although 'top-down' control by predators has been more commonly studied *in situ* than have 'bottom-up' controls in seagrass systems (Heck et al. 2000; Per-Olav et al. 2008), forces from either direction can cause drastic changes in diversity and density of benthic inhabitants resulting in loss of seagrass functions (Fox et al. 2010).

3.6 Conclusion

This study demonstrated some distinct changes in the benthos of Izembek Lagoon that are likely related to seagrass morphological shifts based on increased irradiance and temperature since the 1970's. These changes in the foundation species and the associated ecological repercussions have not been quantified, but documenting patterns of change in subarctic seagrass systems such as Izembek Lagoon is key to forecasting the effects of shifting climate in lower latitudes. The next step, understanding mechanistic drivers behind this shifting benthic community, could be better addressed with several recommendations. For example, while baseline monitoring exists for economically/ecologically important organisms supported by northern latitude seagrass beds (e.g., migratory birds, pollock, Pacific salmon and northern sea otters), estimates of the seagrass primary production underpinning this northern coastal ecosystem have not been established. Neither is there an understanding of the interplay of morphology, patchiness and degradation rates of seagrasses and seagrass beds that would help to elucidate the relationship between biomass and energy turnover as made available to higher trophic levels.

Understanding the effects of community diversity and abundance shifts is critical because over the last few decades human activities have changed local and global species distributions, precipitating what has been called the sixth major extinction event in known history (Chapin et al. 2000). These changes have occurred over a relatively short time period and improvement in our understanding of the driving mechanisms requires urgent attention (Canuel et al. 2007). This is especially critical in coastal transition zones like seagrass ecosystems where the benthic community delivers and supports functions within and outside the seagrass bed (e.g., nutrient transformation, carbon breakdown and sequestration, and support of upper trophic levels; Levin et al. 2001). Stability in high latitude seagrass communities is a topic of increasing concern due to the array of ecosystem services they provide and their immediate exposure to changing climate compared to lower latitude systems. In the next century, there is no question that the sub-arctic and arctic surface seawaters will be warmer, more CO_2 rich, and bear the load of increased commerce, resource extraction and coastal development. Thus, steps toward quantifying a baseline status of northern seagrass communities are critical for effective management strategies in this changing system.

3.7 References

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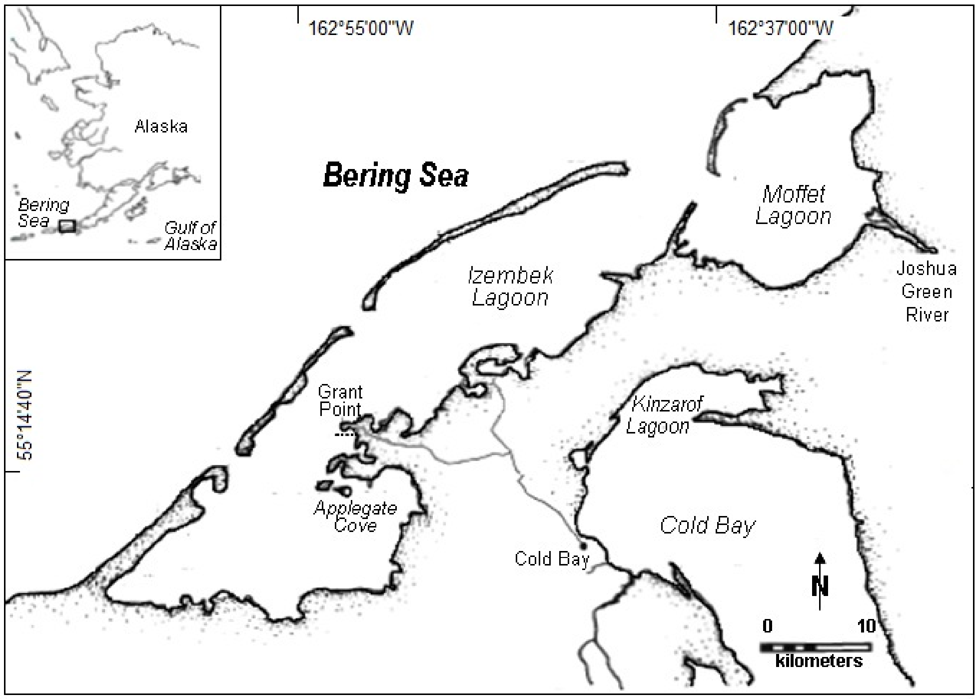

Fig 3.1 Izembek Lagoon region of the Alaska Peninsula. The historic transect used for this study is immediately south of Grant Point (dotted line)

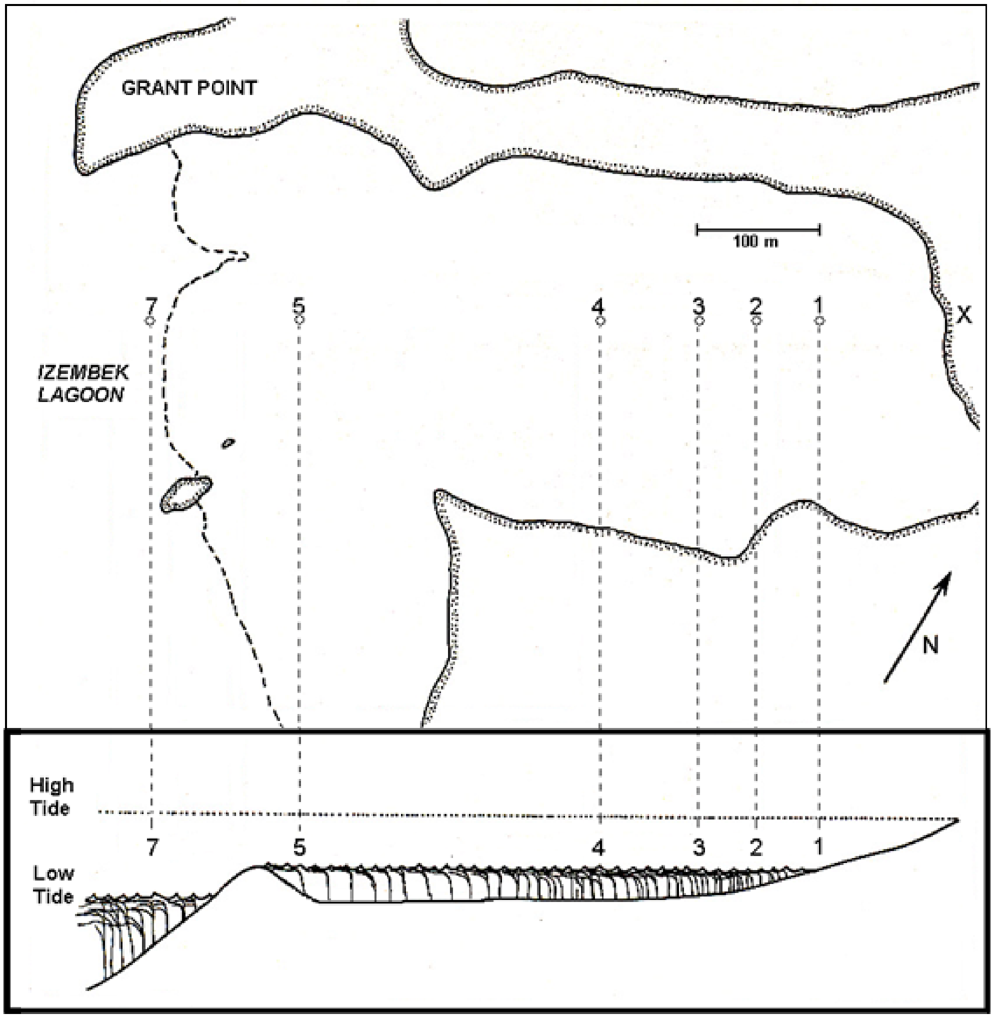

Fig 3.2 Sampling transect at Grant Point showing relative depth strata. Numbers represent stations in 1977 and 2008. The transect begins with a permanent boulder (X) on the beach and becomes progressively deeper along an intertidal bench, ending at subtidal station 7

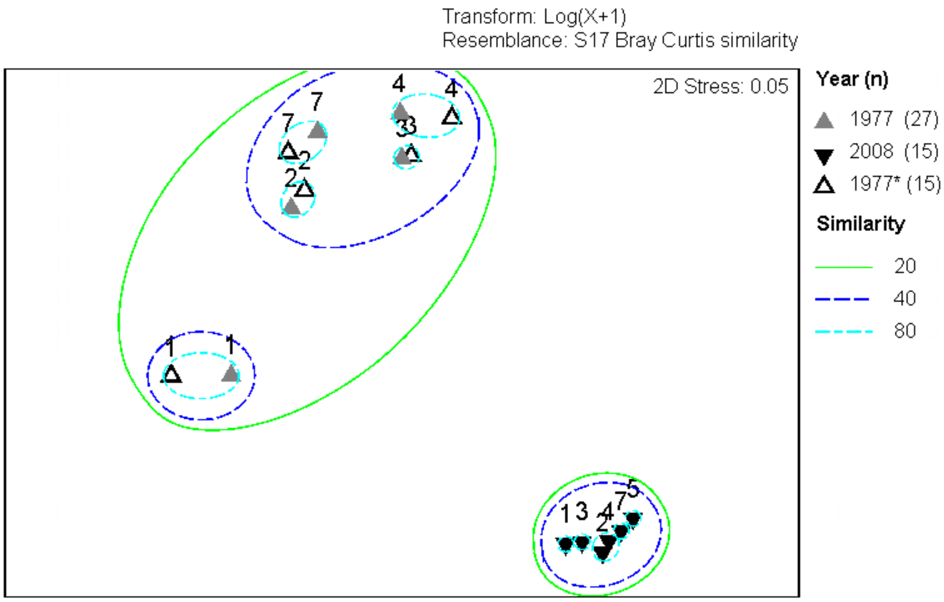

Fig 3.3 Multidimensional scaling shows greater similarities in averaged faunal density per station in the benthic community between 1977 and 1977* groups than between 2008 and either 1977 or 1977*. Station numbers are given next to points, total replicates (n) within a year group are shown in parenthesis. Cluster analysis resulted in a similarity index among stations shown with dash and solid lines

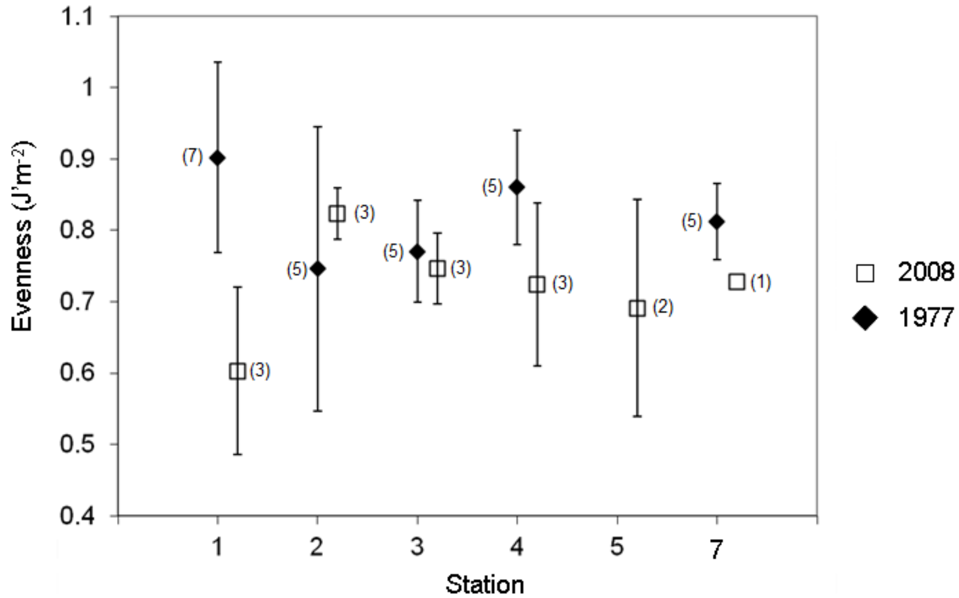

Fig. 3.4 Mean faunal evenness (± 1 SD) in 2008 and 1977 shown with Pielou's index at stations along the sampling transect. Number of replicate samples shown in parenthesis. Where no SD bars are present, sample size is n = 1

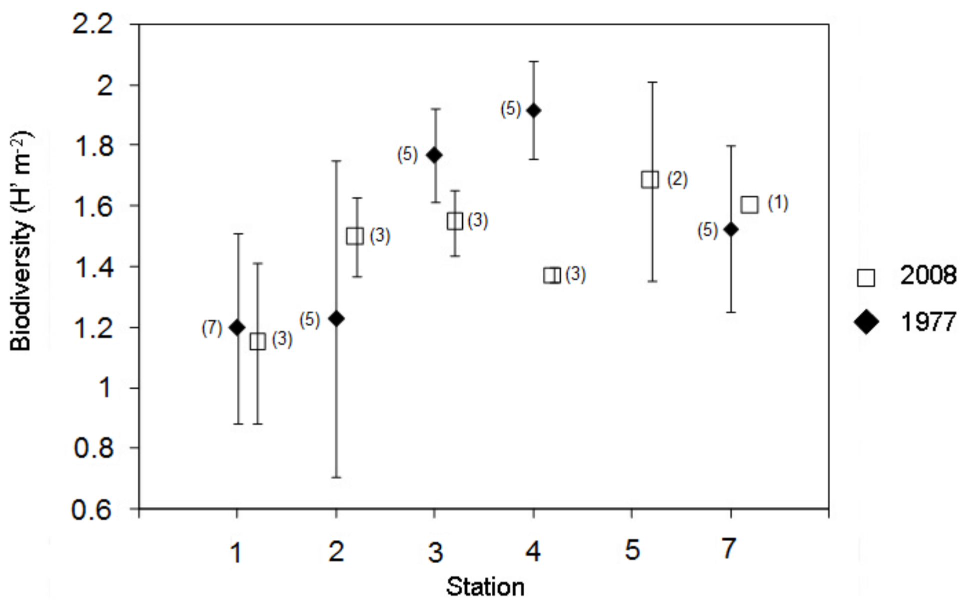

Fig. 3.5 Mean biodiversity (± 1 SD) in 2008 and 1977 shown with the Shannon-Wiener index at stations along the sampling transect. Number of replicate samples shown in parenthesis. Where no SD bars are present, sample size is n = 1

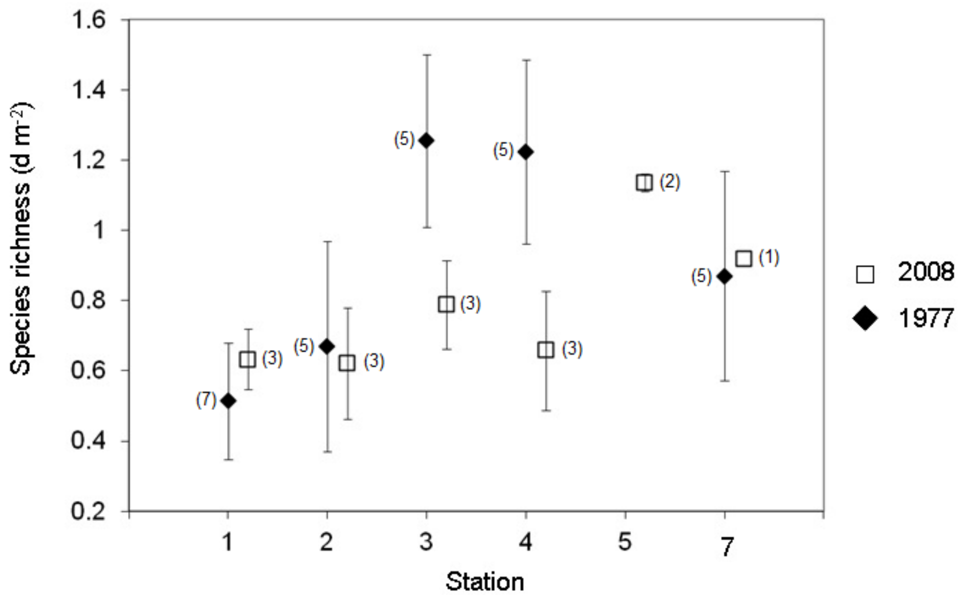

Fig. 3.6 Mean species richness (± 1 SD) in 2008 and 1977 shown with Margalef's index at stations along the sampling transect. Number of replicate samples shown in parenthesis. Where no SD bars are present, sample size is n = 1

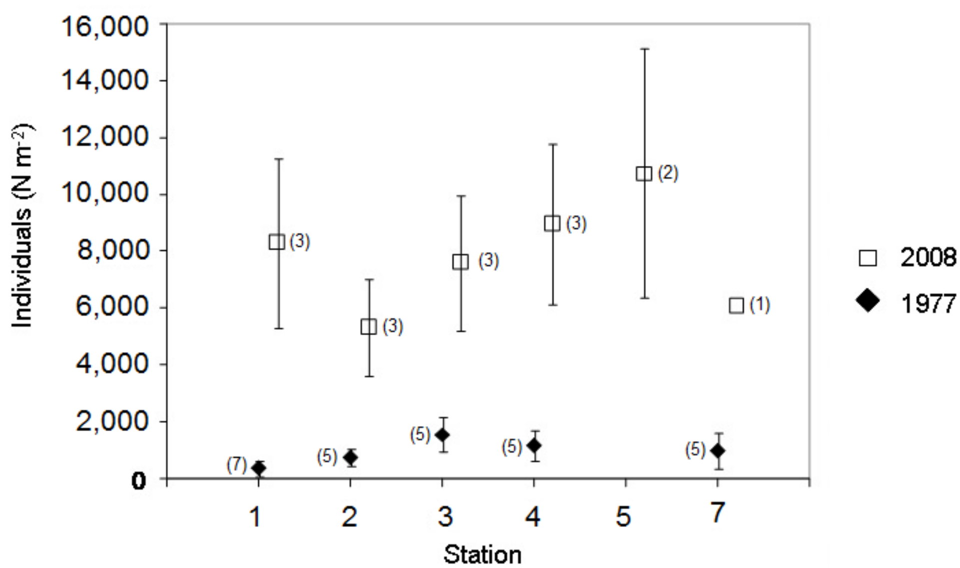

Fig. 3.7 Mean faunal density (± 1 SD) at stations along the sampling transect. Number of replicate samples shown in parenthesis. Where no SD bars are present, sample size is n = 1

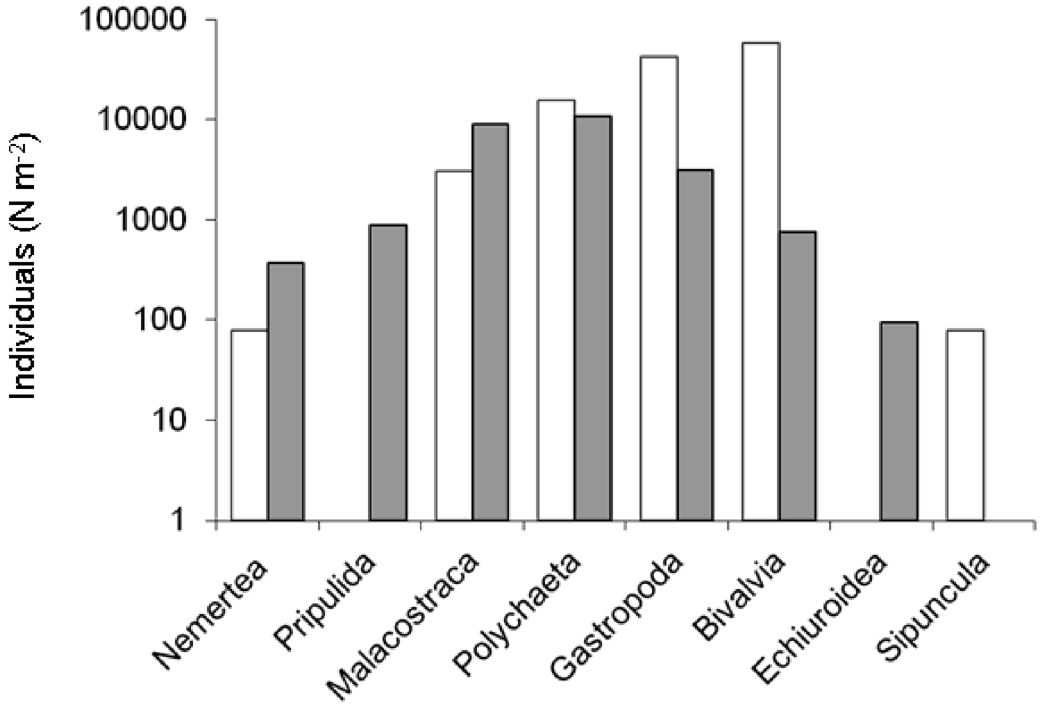

Fig. 3.8 Comparison of aggregated taxonomic group density as recorded from sediment cores in 2008 (white bars, n = 15) and 1977 (grey bars, n = 27). Core samples were extrapolated to reflect density per m^2

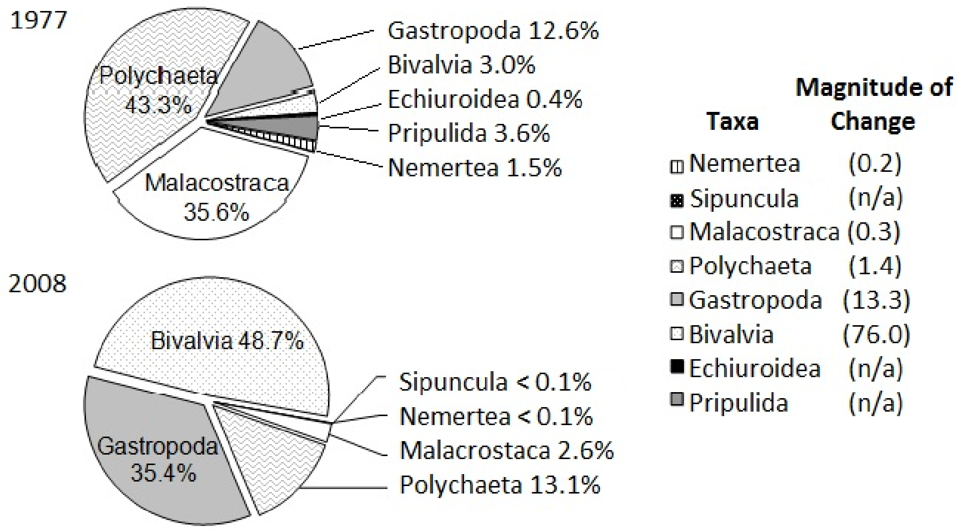

Fig 3.9 Taxon density as a percentage of total individuals sampled in historic (1977) and modern (2008) sediment cores from the Izembek Lagoon benthos. Magnitude of change in taxonomic density over time shown as a ratio of modern over historic taxa densities (2008/1977) in parenthesis

Table 3.1 One-way crossed ANOSIM (Analysis of Similarities) testing similarity of average faunal density between 1977* (rarified 1977 data set), 1977, and 2008 stations on a historic transect.

Pair-wise Test Groups	R Statistic	Significance Level%	Possible Permutations	Actual Permutations
1977*, 2008	0.997	0.2	462	462
1977*, 1977	-0.148	81	126	126
2008, 1977	1.0	0.2	462	462

Table 3.2 One-way ANOVA (Analysis of Variance) tests between common biodiversity indices for benthic community data sets at Izembek Lagoon in 1977 and 1977* (rarified 1977 data set). Significance level was set at $\alpha \leq 0.05$

		SS	*df*	*MS*	*F*	*P-value*	*F crit*
Density (Total Individuals per m^2)							
Variance	*Between Groups*	263977.21	1	263977.21	0.70	0.41	4.08
	Within Groups	15052810.69	40	376320.27			
	Total	15316787.91	41				
Evenness (Pielou)							
Variance	*Between Groups*	0.01	1	0.01	0.79	0.38	4.08
	Within Groups	0.63	40	0.02			
	Total	0.64	41				
Diversity (Shannon-Wiener)							
Variance	*Between Groups*	0.00	1	0.00	0.01	0.92	4.08
	Within Groups	6.89	40	0.17			
	Total	6.89	41				
Richness (Margalef)							
Variance	*Between Groups*	0.01	1	0.01	0.10	0.75	4.08
	Within Groups	5.77	40	0.14			
	Total	5.79	41				
Average Taxonomic Distinctness (Δ^+)							
Variance	*Between Groups*	94.75	1	94.75	0.76	0.39	4.08
	Within Groups	5000.17	40	125.00			
	Total	5094.92	41				

Table 3.3 BEST matching test between 1977 and 2008 for community abundances of taxa. Groups of organisms were compared on a taxonomic class level, or to phyla where class designation was not available

Multiple Random Permutations	Number of Variables Selected	Correlation	Variables Selected
99	1	0.808	Bivalvia
99	5	0.860	Bivalvia, Gastropoda, Malacostraca, Polychaeta, Pripulida

Appendices

Appendix 3.1 Abundance of organisms (individuals per m^2) at stations on the Grant Point long-term transect in 1977 at Izembek Lagoon

Taxa	1977 Station number and (n) replicates				
	1 (7)	2 (5)	3 (5)	4 (5)	7 (5)
Annelida					
Abarenicola pacifica	234	280	0	0	0
Ammotrypane aulogaster	0	0	0	47	0
Anaitides maculata	0	0	0	0	187
Capitella capitata	0	187	93	187	140
Eteone longa	47	47	0	0	47
Haploscoloplos panamensis	0	2336	2290	935	2243
Harmothoe imbricata	47	0	47	47	0
Hesperone complanata	0	47	0	47	0
Naimereis quadricuspida	0	0	0	47	93
Orbinidae	0	0	0	0	93
Pholoe minuta	0	0	47	47	0
Polychaete	0	0	93	0	0
Polydora quadrilobata	0	0	93	47	0
Polynoidae	0	0	47	0	47
Scoloplos armiger	0	0	0	0	187
Terebellides stroemi	0	0	187	187	0
Arthropoda					
Allorchestes angusta	0	0	47	0	0
Amphipod	93	93	140	0	47
Ampithoe simulans	187	140	1121	1215	701
Ampithoidae juveniles	140	0	0	0	0
Anisogammarus sp.	0	0	1121	1495	140
Calliopiella pratti	47	0	0	0	0
Caprellidae	0	0	0	234	93
Corophium sp.	0	93	0	0	93
Crangon septemspinosa	187	0	0	0	0
Cumacean	0	0	0	0	47
Gammaridae	1028	0	47	0	187
Orchomene	0	0	0	0	47
Euseridae	47	0	0	0	0
Mollusca					
Macoma balthica	47	0	47	0	0
Macoma calcarea	47	93	140	47	0
Cingula katharinae	0	0	47	47	0
Cyclichna occulata	0	0	327	47	0
Doxiospira spirillum	0	0	0	47	0
Littorina sitkana	327	234	1262	467	327
Turtonia occidentalis	0	0	47	234	0
Pelecypod	0	0	0	0	47
Nemertea					
Nemertean	93	47	47	47	140
Pripulida					
Priapulus caudatus	0	187	234	421	47
Sipuncula					
Echiurus echiurus	0	47	47	0	0

Appendix 3.2 Abundance of organisms (individuals per m^2) at stations on the Grant Point long-term transect in 2008

Taxa	**2008 Station number and (n) replicates**					
	1 (3)	**2 (3)**	**3 (3)**	**4 (3)**	**5 (2)**	**7 (1)**
Annelida						
Abarenicola pacifica	159	0	0	0	0	0
Eteone longa	0	0	80	0	398	0
Harmothoe imbricata	80	0	159	239	318	80
Orbinidae	1353	557	1750	557	80	0
Maldanidae	1830	1273	1989	1512	716	716
Polychaete10	0	0	0	0	159	0
Polychaete 11	0	0	0	0	0	80
Polychaete 12	0	0	0	0	80	0
Polychaete 7	0	0	80	0	0	0
Polychaete 8	0	0	0	0	955	0
Polychaete 9	0	0	0	0	80	0
Polynoidae	80	0	159	0	0	0
Arthropoda						
Caprella alaskana	0	80	239	1114	1273	80
Caprella sp.	0	0	0	159	0	0
Microjassa sp.	0	80	0	0	0	0
Mollusca						
Boreocingula martyni	398	2069	2944	2546	7241	637
Littorina sitkana	4694	5411	6047	6843	1034	1273
Margarites helicinus	0	0	0	0	477	159
Macoma balthica	318	1114	318	477	398	318
Turtonia occidentalis	15913	5411	8912	13367	8275	2705
Nemertea						
Nemertean 1	80	0	0	0	0	0
Nemertean 2	80	0	0	0	0	0
Nemertean 3	80	0	0	0	0	0
Sipunculida						
Golfingia sp.	0	0	80	0	0	0

Chapter 4: General Conclusions

4.1 Synthesis and Implications for Izembek Lagoon

This thesis investigated the trophic structure and benthic biodiversity of the Izembek Lagoon eelgrass community, located on the north side of the Alaska Peninsula (55º14′40″N, 162º55′00″W). Stable carbon and nitrogen isotope signatures of selected organisms and a community abundance and biodiversity survey of the benthos gave a snapshot of the modern eelgrass food web at Izembek Lagoon. These data were compared to similar data from the mid-1970's (McConnaughey 1978), resulting in a second reference point for monitoring this globally important eelgrass ecosystem. Until recently, comparisons of seagrass food webs on a multi-decadal scale have been uncommon (although see Glemerec et al. 1997; Lotze et al. 2006; Hunt and Nuttle 2007), mirroring a historical lack of awareness for the importance of these foundational ecosystems (Orth et al. 2006). More commonly, comparisons have been made regarding seagrass bed health using historic aerial photos which, unlike Izembek Lagoon's relative areal stability (Ward et al. 1997), show overall seagrass decline with (Short et al.1996; Lotze et al. 2006; Barsanti et al. 2007) and without the presence of anthropogenic stressors (Glemerec et al. 1997 and Wyllie-Echeverria et al. 2003). Temporal comparisons of seagrass food webs are typically limited to fluctuations within a seasonal context (e.g., Danovaro and Gambi 2002; Thom et al. 2003). This is possibly due to a rarity of early isotope studies, but more likely because key seagrass processes (production pulses, photosynthesis, faunal recruitment) are regulated by seasonality.

Chapter 2 presented carbon stable isotope data produced from the analysis of primary producers and fauna from Izembek Lagoon and compared these data with a previous set of carbon stable isotope data from the same site in the 1970's (McConnaughey 1978). Comparison of these data sets illustrated that the proportional contribution of eelgrass primary production relative to phytoplankton to the benthic food web has increased since the 1970's survey. The results at Izembek are exceptional in that the majority of other documented primary production shifts in seagrass ecosystems are toward decreasing seagrass influence (Green and Short 2003; Orth et al. 2006; Baden et al. 2012). Although the present research may suggest anthropogenic climate shifts causing increases in seagrass food web productivity, many studies implicate this is possible due to the positive effects of ocean acidification on seagrass primary production (Palacios and Zimmerman 2007; Hall-Spencer et al. 2008).

Chapter 2 also presented nitrogen stable isotope data that allowed an estimation of trophic structure in the Izembek eelgrass ecosystem. These data will provide a benchmark for future studies and monitoring of the site. Beginning with $\delta^{15}N = 6.2‰$ at the primary-producer level (an average of eelgrass, eelgrass epiphytes and POM), this food web had four trophic levels and taxa were not evenly distributed with 8% of the species sampled from the first trophic level, 59% from the second, 29% from third, and < 3% from the fourth. Izembek's eelgrass ecosystem was similar in trophic structure to others in subtropical Florida Bay (Browder et al. 1998) and the temperate Baltic Sea (Jaschinski et al. 2008), each with four trophic levels. However, where the food web at Izembek is highly reliant on eelgrass detritus, the Baltic eelgrass system had a higher reliance on eelgrass epiphytes. Although massive seagrass diebacks have occurred in Florida Bay in the last five decades, these have not affected the carbon ratio of seagrass to phytoplankton on which the food web relies (Browder et al. 1998). These three examples suggest that organisms within seagrass food webs are both opportunistic (taking advantage of all possible carbon sources), have dietary plasticity (can take advantage of additions or changes in carbon input), and are highly coupled with the microbial-loop (where seagrass detritus is made labile).

Chapter 3 compared the modern (2008) and historic (1970's) benthic community structure at Izembek Lagoon. My research showed that although the overall benthic community at this site has been relatively stable over the last forty years, several alterations have occurred. The most significant alteration was the increased abundance of two epibenthic species: the bivalve *Turtonia sp.* and the gastropod *Boreocinglua martyni*. This chapter also showed that the modern community was less evenly distributed, but was similar to the historic community in biodiversity, and species and taxonomic richness.

Two main patterns emerged from analyses of the data sets presented in chapters 2 and 3. The first pattern that emerged from the stable isotope data sets was an apparent increase in the proportional contribution of eelgrass-derived carbon to benthic fauna. This pattern was detected in detritivores, deposit and filter feeder consumers, and in the coarse taxonomic categories of polychaetes, shrimps and unsegmented worms. Aerial surveys from the 1990's found no significant increase in eelgrass cover across the lagoon since the 1970's historic study (Ward et al. 1997), which means the eelgrass stock is not apparently more expansive. Even so, unpublished data from the U.S. Fish and Wildlife Service imply that eelgrass plants at Izembek may be more foliose now than four decades ago (McRoy and Wendling, unpublished work). More foliose plants may or may not produce more carbon; however, climate data from 1974-2008 show increased irradiance and air temperature in late winter/early spring around Izembek (Angeloff 2011), which would support increased eelgrass production. Regardless, the higher surface area of more foliose plants can alter flow dynamics within the bed (Verduin and Backhaus 2000; Abdeirhman 2003), increase deposition in the water column (Ginsburg and Lowenstam 1958; Scoffin 1970), and has also been shown to add to drifting detritus (Bell et al. 1995). This enhances carbon delivery to onsite decomposers so that more eelgrass carbon is returned to the detrital loop. In this scenario, there is more eelgrass carbon circulating in the lagoon's ecosystem in 2008 than there was in the mid-1970's. The second pattern was a greater abundance of epifauna (*Turtonia sp.* and *Boreocingula martyni*), which would be supported by an increase in more foliose eelgrass plants (i.e., greater leaf surface area for attachment and grazing substrate). High surface area per unit biomass has often been correlated with robustness in seagrass epifaunal communities including species diversity, total epifaunal abundance and species richness (Heck and Westone 1977; Stoner 1980; Attrill et al. 2000).

This research provides an assessment of coastal ecosystem change in a Bering Sea eelgrass bed. The increased usage of eelgrass carbon in the food web indicates bottom-up forcing, similar to some changes in energy flow shown for the Bering Sea shelf ecosystem (e.g., Hunt and Stabeno 2002; Mueter and Litzow 2008). The data provided here also contribute new information on seagrass ecosystem dynamics from a sub-arctic location, which is useful for comparisons with changes occurring in temperate and tropical seagrass communities.

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